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CONTENTS

FLORA OF PANAMA, PART VI

Family 88. Zygophyllaceae *Duncan M. Porter* 1

Family 96. Polygalaceae *Walter H. Lewis & Olga Herrera-MacBryde* 9

FLORA OF PANAMA, PART VIII

Family 161. Menyanthaceae *Thomas S. Elias* 29

Family 167. Boraginaceae *Joan W. Nowicke* 33

Family 169. Labiatae *Joan W. Nowicke & Carl C. Epling* 71

Viable Soil Algae from the Herbarium of the Missouri Botanical Garden *Bruce C. Parker, Noel Schanen & Richard Renner* 113

Scanning Electron Microscopy as an Aid to Pollen Taxonomy *John E. Ridgway & John J. Skvarla* 121

On Tropical Tree Seedlings. I. Seeds, Seedlings, Systems, and Systematics *James A. Duke* 125

Adventive Plants New to the Missouri Flora (III) *Viktor Muehlenbach* 163

Notes on the Galápagos Euphorbieae (Euphorbiaceae) *Derek Burch* . 173

The Genus *Cienfuegosia* Cav. (Malvaceae) *Paul A. Fryxell* . . . 179

The Initiation of Vascular Cambium and Production of Secondary Xylem in Flower Bud Pedicels of *Asclepias curassavica* L. *F. M. Safwat* . . 251

Cytological and Chromatographic Evidence of Interspecific Hybridization in *Petalostemon* *Sally A. Walker* 261

The Genus *Hoffmannia* (Rubiaceae) in Panama *John D. Dwyer* . . 269

NOTES

The Skunk Cabbage in Missouri *Erna R. Eisendrath* 287

Supplementary Notes on the Phytolaccaceae, I. *Joan W. Nowicke* . 288

Kallstroemia (Zygophyllaceae) in Missouri *Duncan M. Porter* . . 290

Tropical Island Biogeography: The Missouri Botanical Garden's Sixteenth Annual Systematics Symposium *Duncan M. Porter* 293

Seasonal Flowering Behavior in Central Panama *Thomas B. Croat* . . . 295

Studies in Neotropical Paleobotany. I. The Oligocene Communities of Puerto Rico *Alan Graham & David M. Jarzen* 308

Wood Anatomy of Goodeniaceae and the Problem of Insular Woodiness *Sherwin Carlquist* 358

The California Islands *Robert F. Thorne* 391

Distribution Patterns of West Indian Mosses *Marshall R. Crosby* . . . 409

Drosophilidae of Hawaii *Hampton L. Carson* 417

Vegetation of a Galápagos Island before and after an Ice Age *Paul A. Colinvaux* 419

Pollen Morphology of Saprophytic Taxa in the Gentianaceae *Siwert Nilsson & John Skvarla* 420

Cytotaxonomic Notes on Some Neotropical Gentianaceae *Richard E. Weaver, Jr.* 439

Spores of the Heterophyllous *Selaginellae* of Mexico and Central America *Robert Lee Hellwig* 444

The Ozark Flora—Some Collections of Note *W. G. D'Arcy* 465

NOTES

Additional Type Material of *Bouvardia* (Rubiaceae) *Will H. Blackwell, Jr. & Marshall C. Johnston* 468

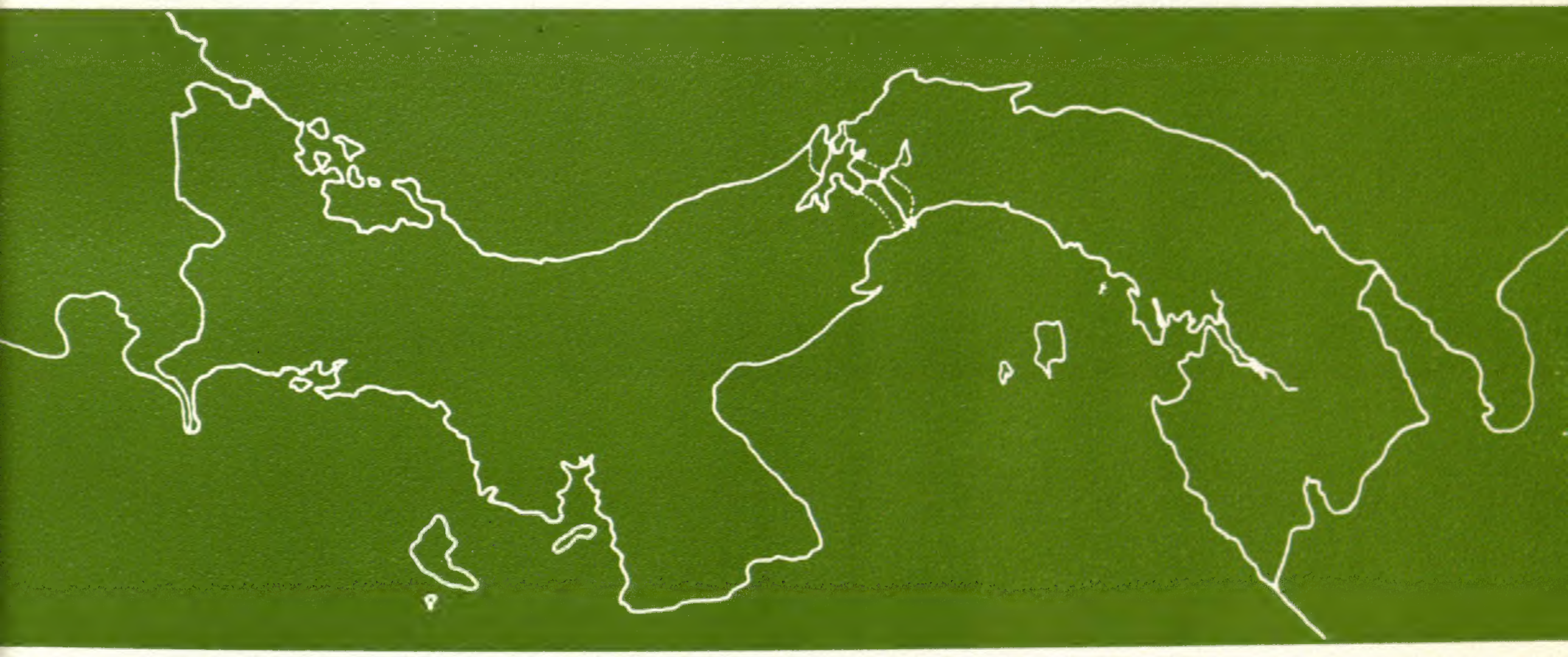
A New Species of *Scaevola* (Goodeniaceae) from Tahiti *Sherwin Carlquist* 469

Chromosome Numbers of Phanerogams. 3. 471

Some new combinations in *Protium* (Burseraceae) *Duncan M. Porter* 475

VOLUME 56
1969
NUMBER 1

ANNALS OF THE
Missouri Botanical Garden



CONTENTS

FLORA OF PANAMA, PART VI

Family 88. *Zygophyllaceae*
by Duncan M. Porter 1-7

Family 96. *Polygalaceae*
by Walter H. Lewis & Olga Herrera-MacBryde 9-28

FLORA OF PANAMA, PART VIII

Family 161. *Menyanthaceae*
by Thomas S. Elias 29-32

Family 167. *Boraginaceae*
by Joan W. Nowicke 33-69

Family 169. *Labiatae*
by Joan W. Nowicke & Carl C. Epling 71-111

VOLUME 56
1969
NUMBER 1

ANNALS OF THE
Missouri Botanical Garden

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VOLUME 56
1969
NUMBER 1

ANNALS OF THE
Missouri Botanical Garden

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 88. ZYGOPHYLLACEAE[1]

BY DUNCAN M. PORTER
Missouri Botanical Garden

Annual to perennial, often suffrutescent, *herbs*, shrubs, or occasionally trees; branches usually divaricate, with angled or swollen nodes, growth sympodial. *Leaves* opposite or occasionally alternate, usually even-pinnate, occasionally simple or 2-foliolate, rarely 3-7-foliolate, often fleshy to coriaceous, petiolate to subsessile, persistent; leaflets usually entire, inequilateral, petiolulate to subsessile; stipules paired, free, foliaceous, fleshy, or spinescent, persistent or rarely deciduous. *Flowers* (4-)5(-6)-merous, bisexual, hypogynous, regular or occasionally slightly irregular; peduncles terminal or pseudaxillary, 1-flowered, solitary or occasionally few to many; sepals (4-)5(-6), free or rarely slightly connate basally, imbricate, persistent or occasionally deciduous; petals (4-)5(-6), free or rarely connate basally, often clawed, sometimes twisted, imbricate or convolute, deciduous, rarely marcescent; extrastaminal and/or intrastaminal disc usually present; stamens in (1-)2(-3) whorls of 5 each, outer whorl usually opposite petals, often alternately unequal in length or sterile, the filaments free, subulate to filiform or rarely winged, frequently glandular or appendaged basally, occasionally outer whorl basally adnate to petals, inserted on or below disc, the anthers 2-loculed, sub-basifixed to versatile, introrse, longitudinally dehiscent; gynoecium (2-)5-carpelled, syncarpous, superior, (2-)5(-12)-lobed and -loculed, sessile or rarely on a short gynophore, the ovules (1-)2-many per locule, pendulous or ascending, anatropous, placentation axile or rarely basal, the style terminal, usually simple, the stigma minutely and obscurely lobed to distinctly ridged. *Fruit* a (2-)5-lobed loculicidal or septicidal capsule or a schizocarp splitting lengthwise into 5 or 10(-12) hard tubercled to spiny or winged mericarps, rarely a drupe or a drupaceous berry; seeds 1(-many) per locule, endosperm present or absent.

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[1]Assisted by National Science Foundation Grant No. GB-5674.

A family of about 27 genera and 250 species, widely distributed, but mainly in the warmer, drier regions of the world. Two genera, *Kallstroemia* Scop. and *Tribulus* L., have been collected in Panama. *Guaiacum sanctum L.*, from the northern Caribbean, is cultivated in Balboa, while *G. officinale* L., from the southern Caribbean, is cultivated in Panama City and the Canal Zone. The latter also has been reported from Bocas del Toro Province by Allen (Ceiba **10:** 35-36, 1964). Although specimens of *Guaiacum* collected in the wild have not been seen from Panama, the genus is included in the key to genera, as *G. officinale* may occur along the Caribbean coast.

Both *Guaiacum officinale (guayacán, iron wood, lignum vitae)* and *G. sanctum (guayacán, lignum vitae)* are widely cultivated in the tropics for their globose growth habits and myriads of blue or purple flowers. Their wood is very hard, tough, and resinous, and *G. officinale,* in particular, has been used to a considerable extent in the manufacture of small turned objects and stern bearings for ships.

a. Herbs; flowers yellow, stamens unappendaged; fruit a schizocarp separating at maturity into 5-10 mericarps.
  b. Fruit tubercled, at maturity separating into 10 mericarps, beak persisting; intrastaminal glands absent ..... 1. *Kallstroemia*
  bb. Fruit spiny, at maturity separating into 5 mericarps, beak falling with mericarps; intrastaminal glands present ..... 2. *Tribulus*
aa. Trees or shrubs; flowers blue or purple, stamens appendaged; fruit a 2-5-lobed loculicidal capsule ..... *Guaiacum*

1. KALLSTROEMIA

Kallstroemia Scop., Introd. 212, 1777.

Ehrenbergia Mart., Nov. Gen. Sp. Brasil. **2:** 72, 1826, non Spreng., Neue Entdeck. **2:** 129, 1821.

Heterozygis Bunge, Mém. Acad. Imp. Sci. St.-Pétersbourg Divers Savans **2:** 82, 1835.

Annual or occasionally perennial *herbs;* stems herbaceous to suffrutescent, diffusely branched, prostrate to decumbent or ascending, terete, somewhat succulent, becoming striate on drying, densely pubescent to glabrate, spreading radially from a central tap root to 1 m or more long. *Leaves* opposite, elliptical to broadly obovate, abruptly even-pinnate, one of each pair alternately smaller or sometimes abortive; leaflets 2-10 pairs, opposite, entire, subsessile, elliptical to broadly oblong or obovate, somewhat unequal in size, those on one side of rachis slightly smaller, lowest pair markedly unequal, terminal pair pointed forward and more falcate, pubescent to glabrate; stipules foliaceous. *Flowers* solitary, pseudaxillary, regular; peduncles emerging from axils of alternately smaller leaves; sepals 5(-6), free, pubescent, persistent or rarely caducous; petals 5(-6), white to bright orange, the base same or green to red, free, spreading hemispherically, fugaceous, usually marcescent, convolute; disc fleshy, annular, obscurely 10(-12)-lobed; stamens 10(-12), 5(-6) opposite petals exterior, somewhat longer, and adnate basally to petals, 5(-6) opposite sepals subtended to exterior by a small bilobed gland, the filaments filiform, subulate, or rarely basally winged, unappendaged, inserted on disc, the anthers globose or ovoid to linear-oblong or rarely linear, those opposite sepals rarely aborting; ovary sessile, 10(-12)-lobed and -loculed, globose or

ovoid or occasionally conical or pyramidal, glabrous to pubescent, the ovules 1 per locule, pendulous, placentation axile, sometimes 1 or more aborting, the style simple, cylindrical to broadly conical, more or less 10(-12)-ridged, persisting to form a beak on fruit, the stigma capitate, oblong, or clavate, 10(-12)-ridged or -lobed, papillose or rarely coarsely canescent, terminal or rarely extending down almost to base of style. *Fruit* 10(-12)-lobed, ovoid, occasionally conical, or rarely pyramidal, glabrous or pubescent, at maturity dividing septicidally and separating from a persistent styliferous axis into 10(-12) or occasionally fewer mericarps; mericarps 1-loculed, 1-seeded, obliquely triangular, wedge-shaped, more or less tuberculate or rugose abaxially; seeds oblong-ovoid, obliquely pendulous, the testa membranaceous, the embyro straight, endosperm absent.

The largest New World genus of the family, with 17 species occurring in warm arid and tropical areas from the southern half of the United States to central Argentina. Also introduced into West Africa and India. The two species found in Panama apparently are indigenous.

a. Ovary and fruit ovoid, glabrous or occasionally strigose basally; sepals ovate, hirsute with appressed to spreading trichomes, in fruit clasping but not entirely covering mature mericarps, only scarious margins becoming involute . . . . . 1. *K. maxima*
aa. Ovary pyramidal, fruit ovoid, both densely appressed short-pilose; sepals lanceolate, hispidulous with fine trichomes of two lengths, spreading from base of mature fruit and appearing linear-lanceolate through margins becoming sharply involute . . . . . 2. *K. pubescens*

1. **Kallstroemia maxima** (L.) Hook. & Arn., Bot. Beechey 282, 1838.

Tribulus maximus L., Sp. Pl. 386, 1753.
T. trijugatus Nutt., Gen. **1**: 277, 1818.
Kallstroemia tribulus Meisn., Pl. Vasc. Gen. **2**: 43, 1837, nom. superfl.
Tribulus decolor Macfad., Fl. Jamaica 186, 1837, nom. superfl.
T. dimidiatus Raf., Autikon Bot. 176, 1840, nom. superfl.
T. trijugus Steudel, Nom. Bot. ed. 2, **2**: 699, 1841, nom. superfl.
T. tuberculatus Sessé & Moc., Fl. Méx. ed. 2, 109, 1894.
Kallstroemia canescens Rydb. in Vail & Rydb., N. Amer. Fl. **25**: 113, 1910.

Annual *herb;* stems prostrate to decumbent, to 1 m long, sericeous and sparingly hirsute with apically-directed white trichomes. *Leaves* obovate, 1-5.5 cm long, 1-3.5 cm wide; leaflets 3-4 pairs, broadly oblong to elliptical, appressed-hirsute to glabrate, margins and veins sericeous, 5-18 mm long, 3-11 mm wide, terminal pair usually largest. *Flowers* ca 1 cm in diam; peduncles to 28 mm long; sepals ovate, 4-5 mm long, 2 mm wide, as long as or little shorter than petals, hirsute with appressed to spreading trichomes, in flower ca as long as style, in fruit clasping but not entirely covering mature mericarps and shorter than beak, only scarious margins becoming involute, persistent; petals yellow, fading orange, obovate, 4-6 mm long, to 6 mm wide, marcescent; ovary ovoid, ca 1 mm in diam, usually glabrous but occasionally strigose basally, the style 2 mm long, cylindrical, base slightly conical, the stigma capitate, ca 1 mm long, obscurely 10-lobed, papillose. *Fruit* ovoid, 4-5 mm in diam, usually glabrous but occasionally strigose basally, the beak 3-6 mm long, glabrous, cylindrical, the base widely conical; mericarps 4 mm high, 1.5 mm wide, abaxially tubercled, cross-ridged, and slightly keeled, sides pitted, adaxial edge angled.

South Carolina, Georgia, Florida, and Texas, Sinaloa and Tamaulipas, Mexico, to Central America, the West Indies, and northern South America. Called *verdolaga* throughout much of Latin America, as it closely resembles *Portulaca oleracea* L. *(Portulacaceae),* the true *verdoga.* The latter is much used by the populations as a potherb. In Panama *Kallstroemia maxima* is known as *hierba de pollo* (fide *Bro. Heriberto* 35).

CANAL ZONE: Gatún, *Cowell 314* (NY), *Bro. Heriberto* 35 (US); Farfan Beach, *Dwyer 6798* (MO); Ancón, *Greenman & Greenman 5019* (MO); Frijoles, railroad track, *Killip* 3445 in part (US); vic of Ancón, *Piper 5815* (US); betw Panama & Corozal, alt 20-30 m, *Pittier 4443* (F, GH, NY, US); Balboa, roadside, *Standley 26103* (US); Chiva Chiva Trail nr Miraflores Lake, disturbed area, *Tyson 1385* (ATTC[1]); Miraflores Locks area, roadside, *Tyson 1609* (ATTC, MO); Pedro Miguel garbage dump, *Tyson & Blum 4017* (ATTC). CHIRIQUI: David airport, disturbed grassland & edge of marsh, alt 25 ft, *Lewis et al. 737* (MO). LOS SANTOS: 5-9 mi from Chitré on rd to Las Tablas, roadside, *Burch et al. 1216* (F, MO); 10 km S of Chitré, *Correa A. 85* (ATTC). PANAMA: Panama, roadsides, *Hayes 728* (BM); Vera Cruz, beach & sandy areas behind, *Lewis et al. 3015* (MO); sabanas N of Panama, *Bro. Paul 526* (US). PROVINCE UNKNOWN: Bahia Soldado, *Cowell 227* (NY); s. loc., *Seemann s.n.* (BM).

2. **Kallstroemia pubescens** (G. Don) Dandy in Keay, Kew Bull. **10:** 138, 1955.—Fig. 1.

Tribulus pubescens G. Don, Gen. Syst. **1:** 769, 1831.
Kallstroemia minor Hook. f. in Hook., Niger. Fl. 269, 1849, nom. superfl.
Tribulus maximus var. *minor* (Hook. f. in Hook.) Oliver, Fl. Trop. Afr. **1:** 284, 1868.
Kallstroemia caribaea Rydb. in Vail & Rydb., N. Amer. Fl. **25:** 111, 1910.
K. glabrata Rydb. in Vail & Rydb., loc. cit. 112.
K. longipes Rydb. in Vail & Rydb., loc. cit. 114.

Annual *herb;* stems prostrate to decumbent, to 1 m long, hirsute and sericeous with apically-directed fine white trichomes. *Leaves* obovate, to 2 cm long and 1 cm wide; leaflets (2-)3 pairs, elliptical to obovate, appressed-hirsute to glabrate, veins and margins more or less sericeous, to 11 mm long and 5 mm wide, terminal pair largest. *Flowers* ca 1 cm in diam; peduncles 5-15 mm long; sepals lanceolate, 3.5-4 mm long, 1.5 mm wide, in flower ca as long as style, hispidulous with fine white trichomes of two lengths, spreading from base of mature fruit and appearing linear-lanceolate through margins becoming sharply involute, persistent; petals yellow, obovate, ca 6 mm long and 5 mm wide, marcescent; ovary pyramidal, 4 mm long including style, densely appressed short-pilose with fine white trichomes, the style stout, conical, the stigma capitate, ca 1 mm long, obscurely 10-lobed, papillose. *Fruit* ovoid, 5-6 mm in diam, densely appressed short-pilose, the beak ca 3 mm long, ca as long as fruit body, short-pilose, cylindrical, the base conical; mericarps 3-4 mm high, ca 1 mm wide, abaxially cross-ridged and tubercled, adaxial edge angled.

Sinaloa and Yucatan, Mexico, to Central America, Puerto Rico, Jamaica, and the Lesser Antilles, northern South America, Ecuador, and Peru. Introduced into Florida, West Africa, and India.

PANAMA: Nueva Gorgona, nr beach, *Duke 4499* (MO).

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[1]This abbreviation indicates the herbarium of the U. S. Army Tropic Test Center, Fort Clayton, Canal Zone.

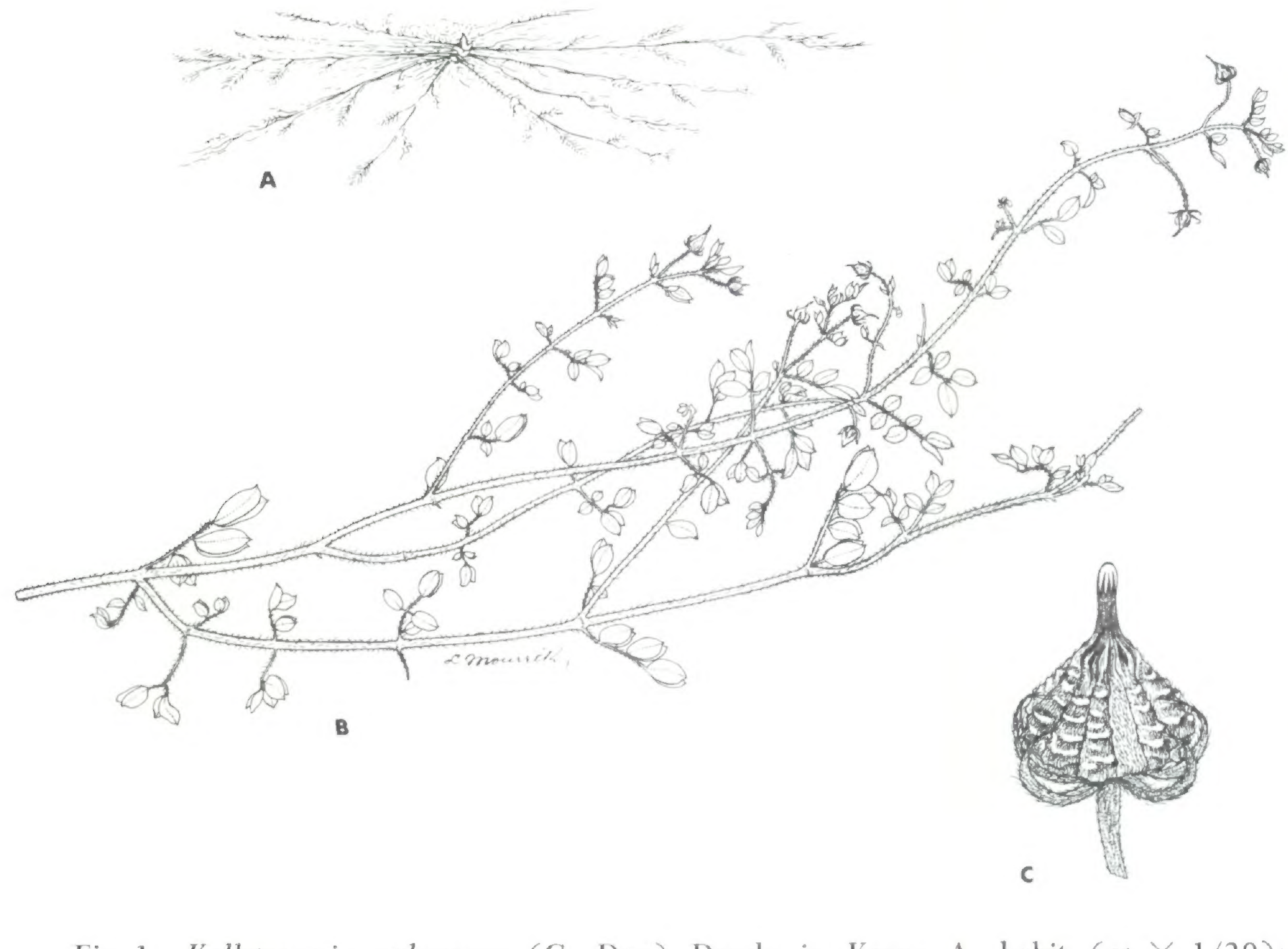

Fig. 1 *Kallstroemia pubescens* (G. Don) Dandy in Keay: A, habit (ca × 1/20); B, branch (× ½); C, fruit (× 3). After *Duke 4499* (MO).

2. TRIBULUS

Tribulus L., Sp. Pl. 386, 1753; Gen. Pl. ed. 5, 183, 1754.

Annual or occasionally perennial *herbs,* very rarely shrubby; stems herbaceous to suffrutescent, diffusely branched, prostrate to decumbent or ascending, terete, somewhat succulent, becoming striate on drying, densely pubescent to glabrate, spreading radially from a central tap root to 3 m long. *Leaves* opposite, elliptical, abruptly even-pinnate, one of each pair alternately smaller or sometimes aborting; leaflets 3-10 pairs, opposite, entire, sessile to very shortly petiolulate, oblong to ovate or elliptical, terminal pair pointed forward, pubescent; stipules foliaceous. *Flowers* solitary, pseudaxillary, regular; peduncles emerging from axils of alternately smaller leaves; sepals 5, free, pubescent, caducous; petals 5, bright yellow or rarely white, the base darker, free, spreading hemispherically, deciduous, imbricate; disc fleshy, annular, 10-lobed; stamens 10, 5 opposite petals exterior, somewhat longer, and adnate basally to petals, 5 opposite sepals subtended to exterior and interior by nectariferous glands, the intrastaminal glands free or connate to form an urceolate ring surrounding ovary base, the filaments filiform

or subulate, unappendaged, inserted on disc, the anthers cordate to sagittate; ovary sessile, 5-lobed and -loculed, ovoid or globose, densely pubescent, the ovules 3-5 per locule, pendulous, superposed in 2 vertical rows on placenta, placentation axile, the style simple, stout, cylindrical, 5-ridged, deciduous, the stigma terminal, pyramidal or globose, 5-lobed, papillose. *Fruit* 5-angled, horizontally depressed, pubescent, at maturity dividing septicidally and separating into 5 or rarely fewer mericarps and leaving no central axis; mericarps broadly triangular, each divided internally by oblique transverse septa into 2-5 1-seeded compartments, spiny or winged or rarely only tuberculate abaxially; seeds oblong-ovoid, obliquely pendulous, horizontally arranged one above the other, the testa membranaceous, the embryo straight, endosperm absent.—$x = 6$.

A genus of the Old World deserts, with perhaps several dozen species. Three species occur as introduced weeds in the Americas; one, *Tribulus terrestris* L., has been collected in Panama. A second, *T. cistoides* L., is to be expected on the isthmus. The latter is a pantropical weed especially common in the Caribbean region and tropical Mexico. It is larger and more erect than *T. terrestris* and has flowers 1.5-4 cm in diameter. *Tribulus cistoides* is usually found in sandy maritime habitats.

1. **Tribulus terrestris** L., Sp. Pl. 387, 1753.

Prostrate *annual;* herbage whitish-pubescent, especially young shoots, becoming glabrate on older parts; stems more or less hirsute and sericeous, to 1 m long. *Leaves* 2-4.5 cm long, ca 1 cm wide; leaflets 4-6(-8) pairs, subsessile, ovate to elliptic, inequilateral, unequal, acute or obtuse, middle pairs largest, densely appressed silky-pubescent giving younger parts a silvery appearance, becoming glabrate, largest 4-11 mm long, 2-4 mm wide; stipules subulate to falcate, pubescent, 1-5 mm long, to 1 mm wide. *Buds* ovoid, obtuse, 2-3 mm long. *Flowers* 5-10 mm in diam; peduncles shorter to longer than shortest pair of leaves, hirsute and strigose, bent but little thickened distally in fruit, 2-7 mm long in flower, 5-15 mm long in fruit; sepals ovate-lanceolate, acute, hirsute, the margins scarious, minutely ciliate, 2-4 mm long, 1.5-2 mm wide; petals yellow, oblong, 2.5-5 mm long, 1-3 mm wide; outer nectaries more or less bilobed, yellowish; stamens with filaments subulate, 2-3 mm long, the anthers cordate, versatile, 1 mm long; inner whorl of nectaries triangular, yellow, free; ovary hirsute with stiff upward-spreading bulbous-based trichomes, 1-5 mm high, the style 1-1.5 mm long, the stigma globose, slightly asymmetrical, ca 1 mm in diam. *Fruit* 10-15 mm in diam excluding spines, 4-12 mm high; mericarps dorsally crested and tuberculate, bearing 2 conical spreading dorsal spines 3-7 mm long and 2 smaller spines near base directed downward or latter absent, hispid and densely sericeous to strigose or almost glabrate, gray to green, sometimes 1 or more aborting.

It is impossible to list the synonomy for this species at present; however, a majority of the names published in the genus probably are referable to it.

This native of the Mediterranean region is a wide-spread weed in the warm-temperate areas of the world. It has been collected only rarely in the New World tropics.

CANAL ZONE: railroad track, Frijoles, *Killip* 3445 in part (US).

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

Ehrenbergia 2
Guaiacum 2†
  officinale 2†
  sanctum 2†
Heterozygis 2
Kallstroemia 2†, **2**
  canescens 3
  caribaea 4
  glabrata 4
  longpipes 4
  maxima **3**, 4†
  minor 4
  pubescens **4**
  tribulus 3
Portulacaceae 4†
Portulaca oleracea 4†
Tribulus 2†, **5**
  cistoides 6†
  decolor 3
  dimidiatus 3
  maximus 3
  —var. minor 4
  pubescens 4
  terrestris 6†, **6**
  trijugatus 3
  trijugus 3
  tuberculatus 3

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 96. POLYGALACEAE[1]

BY WALTER H. LEWIS AND OLGA HERRERA-MACBRYDE
Missouri Botanical Garden, St. Louis

Herbs, erect or scandent shrubs, or rarely small trees. *Leaves* alternate, sometimes opposite or verticillate, simple; stipules absent. *Flowers* ☿, ± zygomorphic, usually racemose, bracteate; sepals 5, unequal (slightly unequal in *Moutabea*), the 2 inner large and often petaloid, wing-like; petals 3 or sometimes 5, declinate, if 3 the lower usually keel-shaped, often appendaged, the 2 upper ligulate or ovate, usually adnate to the lower petal and connate to the staminal sheath, if 5 connate above the middle into a tube and adnate with the sepals, subequal; stamens 8, rarely fewer, the filaments connate for most of their length to form a sheath which may split above, often adnate to the petals or corolla-tube (in *Moutabea*), the anthers erect or pendent, usually dehiscent by an apical pore; ovary superior, (1-)2-5-locular, the style simple, the ovules usually 1 per locule, pendulous. *Fruit* a capsule, drupe, berry, or samara, dehiscent or indehiscent; seeds 1 per locule, rarely 2, often pilose, usually arillate, the endosperm straight.

Eighteen genera with over 1000 species; temperate and tropical regions. Four genera are recognized in Panama with *Polygala* by far the largest. (Keys and description are based largely on Panamanian material.)

a. Calyx free, the sepals unequal with the 2 inner sepals (wings) larger, petaloid; petals 3; ovary 1-2-locular.
  b. Ovary and fruit 2-locular, the fruit a dehiscent capsule; mostly delicate herbs ..... 1. *Polygala*
  bb. Ovary and fruit 1-locular, the fruit indehiscent; mostly somewhat woody.
    c. Scandent shrubs; keel clawed with a fimbriate crest, plicate; fruit a samara with a large wing; lowlands, occasionally cloud forests ..... 2. *Securidaca*
    cc. Erect herbs, shrubs, or rarely trees; keel neither plicate, clawed, nor appendaged; fruit drupaceous, not at all or only very obscurely winged; cloud forests only ..... 3. *Monnina*

aa. Calyx adnate to the corolla, the sepals ± equal, not petaloid; petals 5; ovary (2-)4-5-locular ..... 4. *Moutabea*

1. POLYGALA

Polygala L., Sp. Pl. 701, 1753.

Shrubs, subshrubs, or commonly herbs in Panama. *Leaves* alternate, sometimes opposite or verticillate, simple, short-petioled or sessile. *Racemes* terminal or lateral, sometimes contracted into heads. *Flowers* often showy; sepals 5, unequal, the outer 3 herbaceous, free or sometimes 2 connate basally, the inner 2

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large, petaloid, wing-like; petals 3, connate basally, the lower keel-shaped, crested, lobed, or occasionally unappendaged, the 2 upper ligulate to ovate, connate to the keel or adnate to the staminal sheath or both; stamens 8, the filaments connate nearly to the apex into a sheath split above and adnate to the petals below; ovary 2-locular, the ovules solitary, the style incurved, the stigma dilated, entire to 2-lobed, often tufted. *Capsules* usually membranous, compressed, obovate to orbicular, generally wingless, loculicidally dehiscent; seeds usually 2, often pilose, mostly arillate, with or without endosperm.

A genus of perhaps 500 species, ± cosmopolitan; 13 are recognized in Panama.

a. Leaves alternate (those of the basal ¼ of plant usually verticillate or subverticillate).
  b. Leaves linear-lanceolate to elliptic or ovate, 2-35 mm wide; keel without appendages.
    c. Annual; leaves linear to linear-lanceolate, sometimes elliptic, 1-4.5 cm long, 2-9 mm wide; outer sepals oblong-ovate, obtuse, usually glandular-ciliate on the margin, the larger one 1.8-2.2 mm long, the smaller 2 almost entirely connate, 1.5-1.9 mm long; capsule oblong-ellipsoid, 2.9-3.5 mm long, glabrous; seeds 1.9-2.5 mm long; aril corneous, crest-like, with 2 short appendages, 0.6-0.8 mm long, glabrous . . . . . 1. *P. brizoides*
    cc. Suffruticulose; leaves elliptic to ovate, 2.5-8 cm long, 1-3.5 cm wide; outer sepals lanceolate, acute or acuminate, spreading pilose, usually all 3 ca the same size, 3-5 mm long; capsule ovoid to orbicular, 7.5-11 mm long, spreading pilose; seeds 3.5-5 mm long; aril thin, umbraculiform, without appendages, 2.5-4 mm long, somewhat pilose . . . . . 2. *P. panamensis*
  bb. Leaves narrowly linear or linear-lanceolate, 0.2-3.5 mm wide; keel with appendages.
    d. Racemes elongate, loosely flowered, to 8 cm long.
      e. Flowers white; seeds ca 1 mm long, with a few weakly hook-tipped hairs; aril obsolete; rare . . . . . 3. *P. fendleri* var. *heterothrix*
      ee. Flowers rose to purplish, rarely white; seeds 1-1.8 mm long, with all hairs straight; aril present.
        f. Stems glabrous; seeds 1-1.3 mm long; aril barely 2-lobed, ca 1/10 as long as the seed; occasional . . . . . 4. *P. leptocaulis*
        ff. Stems densely pedicillate-glandular; seeds 1.4-1.8 mm long; aril strongly 2-lobed, ¼-½ as long as the seed; very common . . . . . 5. *P. paniculata*
    dd. Racemes compact, densely flowered, to 2.6 cm long.
      g. Keel not gland-dotted; capsule suborbicular; seeds ellipsoid, sparsely short-pubescent, the 2 lobes of the aril 0.9-1.6 mm long . . . . 6. *P. hygrophila*
      gg. Keel gland-dotted apically and basally; capsule ovoid-oblong; seeds conical, sericeous, comose basally, the 2 lobes of the aril 0.5 mm long to absent.
        h. Wings strongly cuspidate apically; seeds 1.8-2.5 mm long (including coma); aril minute or absent; frequent . . . . . 7. *P. longicaulis*
        hh. Wings not or rarely bluntly mucronate apically; seeds 2.5-2.7 mm long (including coma); aril 2-lobed, 0.5 mm long; rare . . . . . 8. *P. variabilis*

aa. Leaves all verticillate (rarely alternate in apical ¼ of *P. timoutou*).
  i. Mostly delicate herbs to 0.3 m tall; leaves 4-21 mm long, 2.7-8 mm wide; seeds 1-1.8 mm long, lobes of the aril narrowly oblong, 0.9-1.6 mm long.
    j. Racemes compact, very densely flowered, 8-11 mm wide; sepals acuminate apically, 1.5-2.4 mm long; wing much larger than the keel, mucronate at the rounded apex, 3-4.6 mm long, 1.8-3.2 mm wide . . . . . 9. *P. timoutou*

jj. Racemes loose or somewhat densely flowered, 4-6 mm wide; sepals obtuse apically (the lower 2 often somewhat acute in *P. aparinoides*), 0.7-2 mm long; wings ca the same length as the keel, not mucronate at the rounded apex, 1.6-2 mm long, 1-1.2 mm wide.
k. Margin of leaves denticulate; seeds often equaled by the 2 narrowly oblong lobes of the aril . . . . . 10. *P. aparinoides*
kk. Margin of leaves entire or rarely remotely crenate; lobes of the aril ca half the length of the seed . . . . . 11. *P. asperuloides*
ii. Suffrutescent perennials to 2 m tall; leaves 4-7.5 cm long, 1.8-3 cm wide; seeds 4 mm long, lobes of the aril wide, 2.5-3 mm long.
l. Leaves apically acute, sparingly punctate; sepals without glands; aril lobes broadly obovate . . . . . 12. *P. wurdackiana*
ll. Leaves apically acuminate, densely punctate; smaller pair of sepals each with 2 large glands; aril lobes oblong . . . . . 13. *P. jefensis*

1. **Polygala brizoides** St.-Hil., Fl. Bras. Merid. **2:** 30, *t.* 88, 1829.

P. angustifolia H.B.K., Nov. Gen. Sp. Pl. **5:** 405, *t. 511,* 1823, non Gilib. (Fl. Lituan. **2:** 11-3, 1781).

Erect or ± ascending, simple or branched *annuals,* 6-39 cm high; stems terete, ± densely incurved- or loosely-spreading incurved-pubescent. *Leaves* alternate, linear to linear-lanceolate, sometimes elliptic, acute, acuminate or mucronate, rarely obtuse apically, acute or acuminate basally, the lateral nerves 3-6 pairs or obsolete (then 1-nerved), sparsely incurved-pubescent or glabrescent, 1-4.5 cm long, 2-9 mm wide; petioles 0.7-2 mm long. *Racemes* loosely flowered, including the axis to 8 cm long; bracts deciduous, ovate-lanceolate, acute, the margin ciliate, 1-1.8 mm long. *Flowers* purple, greenish-white, or greenish-lavender, on slender pendulous pedicels, 1.2-1.5 mm long; outer sepals oblong-ovate, obtuse, usually glandular-ciliate on the margin, rarely eglandular, the largest 1.8-2.2 mm long, the smaller 2 almost entirely connate, 1.5-1.9 mm long; wings unequal, broadly obovate, retuse apically, cuneate basally, the margin somewhat undulate, obscurely flabellinerved, glabrous, 3.2-4 mm long, 2.5-3.4 mm wide; upper petals angustate in the middle, suborbicular-obovate, 3-3.2 mm long, retuse apically, the margin often undulate, the basal half ± hairy inside; keel 3.5-4 mm long without appendages; staminal tube sparsely pubescent basally or glabrescent, the filaments 1.4-1.6 mm long; ovary oblong, 0.9-1.5 mm long, 0.8-1.1 mm wide, the style curved, 2.4-2.7 mm long, the stigma lateral, concave, villous-ciliate. *Capsules* oblong-ellipsoid, 2.9-3.5 mm long, 2.1-2.8 mm wide, glabrous; seeds (Fig. 1c) oblong, 1.9-2.5 mm long, densely pilose; aril corneous, crest-like at the top of the seed with 2 short appendages, 0.6-0.8 mm long, glabrous.

Mexico to Paraguay and the West Indies.

CANAL ZONE: Pipeline Rd, at end of rd, nr Gatun Lake, *Croat 4728* (MO); Ft Kobbe nr BOQ, *Duke 3934* (MO); Sosa Hill, *Duke 4649* (MO); rd to Corozal, *Gervais 144* (US); Balboa Heights, dry hillsides, *Killip 3062* (US); W slope of Ancon Hill, vic of Balboa, alt 20-75 m, *Seibert* 382 (GH, MO); Balboa, moist thicket, scarce, *Standley 25467* (US), weedy field, *Standley 25661* (US), moist thicket, *Standley 28323* (US). CHIRIQUI: Boquete, savannas, alt 4000 ft, *Davidson 754* (MO, US); David airport, disturbed grassland & edge of marsh, alt 25 ft, *Lewis et al. 770* (MO), *773* (MO); Sabana de la Tortuga, betw El Boquete & Caldera, alt 300-700 m, *Pittier* 3337 (MO); vic of Boquete, Llanos Francia, alt 3300 ft, *Stern et al. 1171* (MO). COCLE: vic of Nata, alt 50 m, *Allen 834* (GH, MO, US); Río Hato Airstrip, *Blum & Dwyer 2464* (MO); El Valle, ca 3.6 km from El Greco Hotel along rd to InterAmerican Hwy, *Correa & Dressler*

1012 (MO); Aguadulce, savannas, nr sea level, *Pittier 4867* (US); betw Las Margaritas & El Valle, *Woodson et al. 1272* (GH, MO, NY). PANAMA: savanna nr Río Pacora & Chepo Hwy, *Duke* 5935 (MO); along rd toward top of Cerro Campana, bald savanna-like areas, *Duke 5952* (MO); nr Chepo, savannas, *Duke* 6052 (MO); Cerro Campana, grassland, *Ebinger 944* (MO); San José I, East Harbor, rocky coastal bluffs, *Erlanson 441* (GH, MO), grassy bluffs, *Erlanson* 583 (GH, MO); Tumba-Muerto, *Bro. Heriberto 187* (US); N of Panama City, savannas, *Bro. Paul 521* (US); Sabana de Juan Corso, nr Chepo, alt 60-80 m, *Pittier 4506* (US), *Pittier 4743a* (US); Laguna de Portalla, nr Chepo, alt 50 m, *Pittier 4635* (US); vic of Juan Franco Race Track, savanna, scarce, *Standley 27728* (US); E of Pacora, wet savanna, alt ca 25 m, *Woodson et al. 753* (MO); nr Arraiján, thickets & forests, alt ca 15 m, *Woodson et al. 1373* (GH, MO, NY, US).

Considered a variety of *P. monticola* H.B.K. by Steyermark (Fieldiana: Bot. **28:** 300, 1952).

2. **Polygala panamensis** Chodat, Mém. Soc. Phys. Genève **31**(2): 35, 1893.

Suffruticulose; stems several, branching, 15-68 cm long, pilose. *Leaves* alternate, elliptic to ovate, acute or acuminate apically, cuneate basally, (the lower sometimes oval and obtuse), with ca 5 pairs of lateral nerves, somewhat reticulate, pilose above and beneath, usually more densely so along the veins beneath, 2.5-8 cm long, 1-3.5 cm wide; petioles 1-2 mm long, pilose. *Racemes* loosely flowered, 2-10 cm long (including the short axis), densely pilose; bracts deciduous, linear to linear-lanceolate, pilose, 1.8-3 mm long. *Flowers* blue or purple, the pedicels 1.5-3.3 mm long; outer sepals lanceolate, acute or acuminate, spreading pilose, all 3 ca equal, 3-5 mm long (occasionally 1 to 0.5 mm longer); wings oblong, rounded apically, cuneate basally, pilose along the costa, 7-10 mm long, 3.8-5 mm wide; upper petals narrowly obovate-spatulate, ciliate below or glabrescent, equaling the keel; keel 6.5-8 mm long, without appendages; staminal tube slightly split to ca halfway into 2 bundles each of 4 partly free filaments, the filaments 1.5-2.2 mm long; ovary oblong, 1.5-3.5 mm long, 0.8-1.1 mm wide, pubescent, the style curved, 3.2-4.5 mm long, the stigmas 2, slightly spaced, the outer subapical on a small stalk, the inner sessile. *Capsules* ovoid to orbicular, 7.5-11 mm long, 6.5-10 mm wide, spreading-pilose; seeds (Fig. 1i) flattened, 3.5-5 mm long, pilose; aril membranaceous, umbraculiform, 2.5-4 mm long, pilose, the margin irregularly toothed.

Panama.

CHIRIQUI: vic of El Boquete, alt 1000-1500 m, *Cornman 2054* (US); Boquete, savannas, alt 4000 ft, *Davidson 749* (MO); El Boquete, roadside, alt 1300 m, *Killip 3501* (US); vic of Boquete to 3 mi N, alt 3300-4200 ft, second growth, cultivated areas & roadsides, *Lewis et al. 375* (MO); El Boquete, pastures, alt 1000-1300 m, *Pittier 2891* (NY, US); betw Cerro Vaca & Hato del Loro, 850-1100 ft, *Pittier* 5394 (F, GH, US); Río Chiriquí Viejo Valley, nr El Volcán, *White 232* (GH, MO, US); valley of upper Río Chiriquí Viejo, *White & White 102* (MO). COCLE: vic of El Valle, alt 600-1000 m, *Allen 1153* (MO); vic of Olá, alt 100-350 m, *Pittier 5077* (US).

Closely related to if not conspecific with *P. costaricensis* Chodat and *P. durandii* Chodat of Guatemala and Costa Rica.

3. **Polygala fendleri** Chodat var. **heterothrix** Blake, Bull. Torrey Bot. Club, **51:** 85, 1924.

Erect, very slender, usually branched *annual;* 6-15 cm high; stems ribbed, glabrous. *Leaves* whorled in 3-4's at the base of the stem, lance-obovate, 3-5 mm

long, 1-1.8 mm wide, the upper alternate, linear or linear-lanceolate, 4-10 mm long, 0.4-1.5 mm wide, acute to cuspidate, 1-nerved, the margins slightly revolute, glabrous, subsessile. *Racemes* loosely flowered, cylindric, to 7 cm long, 5.5-6.5 mm wide, the axis to 3 cm long; bracts deciduous, linear-lanceolate, acute, glabrous, 0.8-1.1 mm long. *Flowers* white, the pedicels to 0.8 mm long; largest sepal broadly ovate to suborbicular, rounded, 0.9-1.1 mm long, the smaller 2 oblong, obtuse, 0.8-1 mm long; wings elliptic or subobovate, rounded apically, short-cuneate basally, 2.2-3 mm long, 1.2-2.1 mm wide; upper petals oblong, rounded, equaling the keel; keel 2-2.6 mm long, 4-lobed, the lobes 0.6-0.8 mm long; staminal tube glabrous inside, anthers subsessile; ovary suborbicular, 0.5-0.7 mm long, 0.4-0.6 mm wide, the style ascendent, 0.5-0.7 mm long, developed distally into a navicular cavity, the inner end of which has a sessile, globose stigma. *Capsules* narrowly ellipsoid, 1.8-2 mm long, 1 mm wide; seeds (Fig. 1d) ca 1 mm long, the hairs mostly straight, a few weakly hook-tipped; aril obsolete.

Panama.

CHIRIQUI: Boquete, Llanos Francia, 4 mi from Boquete toward Dolega, llanos bordering creek, alt ca 4500 ft, *Duyer & Hayden 7618A* (MO). COCLE: vic of El Valle de Antón, alt ca 600 m, *Allen 1933* (MO, US); betw Las Margaritas & El Valle, open llano, *Woodson et al. 1261* (MO, US).

4. **Polygala leptocaulis** Torrey & Gray, Fl. N. Amer. **1:** 130, 1838.

Erect, simple and usually slender *annuals;* 12-40 cm high; stems subangulate, glabrous. *Leaves* alternate, linear, acute to acuminate, 1-nerved, the margins slightly revolute, glabrous, 4-25 mm long, 0.2-1 mm wide, subsessile. *Racemes* cylindric, loosely flowered, 1-8 cm long, 5-5.5 mm wide, the axis to 10 cm long; bracts deciduous, lanceolate, acute, glabrous, 0.7-1.2 mm long. *Flowers* deep rose, the pedicels 2 mm long; outer sepals 0.8-1 mm long, the largest broadly ovate, the smaller 2 ovate to oblong; wings obovate or elliptic, rounded apically, cuneate basally, 3-nerved, 1.8-2 mm long, 0.7.0-9 mm wide; upper petals oblong or ovate, usually emarginate at the somewhat narrowed apex, 1.7-1.9 mm long; keel 1.3-1.7 mm long, the crest 5-10-lobed, the lobes 0.2-0.7 mm long, usually single, sometimes forked apically; staminal tube glabrous inside, the filaments very short; ovary oblong or ovoid, 0.3-0.6 mm long, 0.2-0.3 mm wide, the style minute, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose, sessile stigma. *Capsules* oblong, with a row of glands on each side of the septum, 1.5-1.8 mm long, 0.7-0.9 mm wide; seeds (Fig. 1g) oblong, 1-1.3 mm long, sparsely appressed-pubescent, aril minute, 2-lobed, appressed, ca 1/10 as long as the seed, glabrous.

Louisiana and throughout Central America and the West Indies to northern Argentina. Frequently confused with *P. paniculata* L.

CANAL ZONE: Chiva-Chiva, dry fields, *Killip 3128* (MO, US). CHIRIQUI: Llanos Francia, vic of Boquete, alt 3300 ft, *Stern et al. 1158* (GH, MO, US); vic of Boquete, rooted in water, alt 1200-1500 m, *Woodson & Schery 781* (MO). COCLE: vic of El Valle, alt 800-1000 m, *Allen 99* (MO); El Valle de Antón, along Río Antón, lower portion of valley & marshes, alt ca 500 m, *Hunter & Allen 376* (MO); Picacho de Olá, alt 350-600 m, *Pittier 5070* (US); El Valle de Antón & vic, on tussocks in bogs, alt 500-700 m, *Seibert*

488 (GH, MO, NY, US). PANAMA: along rd betw Panama & Chepo, in savannas, *Dodge et al. 16691* (MO); nr Río Pacora & Chepo Hwy, savanna, *Duke* 5936 (MO), 5942 (MO); Tocumen, field, *Dwyer* 2569 (MO); Tocumen airport, *Dwyer* 2583*a* (GH); Pacora, *Méndez 107* (MO); E of Pacora, wet savanna, alt ca 25 m, *Woodson et al. 731* (GH, MO, US).

5. **Polygala paniculata** L., Syst. Nat. ed. 10, 1154, 1759.

Erect, mostly much-branched *annuals,* 10-50 cm high; stems terete, densely pedicellate-glandular. *Leaves* 4-5-whorled or pseudowhorled at the base of the stem, otherwise alternate, lanceolate to linear-lanceolate, acute apically, cuneate basally, 1-nerved, 5-32 mm long, 0.6-3.5 mm wide, short petioled. *Racemes* cylindric, loosely flowered, 3-7 cm long, 5-7 mm wide, the peduncle to 14 cm long; bracts deciduous, lanceolate, acute, glabrous, 0.8-1.1 mm long. *Flowers* rose or purplish, rarely white, the pedicels 0.7-1.2 mm long; outer sepals bearing 2 glands basally, the largest sepal broadly ovate, obtuse, 1-1.2 mm long, the smaller 2 oblong-ovate, obtuse, 0.9-1.1 mm long; wings obovate, spatulate-obovate or oblong-obovate, rounded apically, cuneate basally, 3-nerved, 2-2.8 mm long, 0.7-1 mm wide; upper petals narrowly ovate-lanceolate, attenuate to the apex, 2-2.5 mm long; keel 1.9-2.7 mm long, the crest 6-10-lobed, the lobes 0.4-0.9 mm long, rarely partly forked apically; staminal tube glabrous inside, the filaments very short; ovary obovoid to almost orbicular, 0.6-0.8 mm long, 0.4-0.6 mm wide, the style straight or ascending, 0.4-0.8 mm long, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose, sessile stigma. *Capsules* ellipsoid to oblong, 1.8-2.6 mm long, 0.9-1.5 mm wide; seeds (Fig. 1j) oblong, 1.4-1.8 mm long, shortly appressed-pubescent, the 2 lobes of the aril narrowly oblong, appressed, 0.4-0.8 mm long.

A pantropical weed; in the Americas extending from Texas to southern Brazil. The species is very common in Panama from sea level to at least 2300 m.

BOCAS DEL TORO: s. loc., *Carleton 126* (GH, NY, US); Changuinola to 5 mi S at jct of Ríos Changuinola & Terebe, edge of river & railway, & adjacent rain forest, alt 100-200 ft, *Lewis et al. 798* (MO). CANAL ZONE: Barro Colorado I, *Avilés 70* (F, MO), *943* (F); Ft San Lorenzo, *Burch et al. 1026* (MO); Ancon, *Celestine 59* (US); nr BOQ, Ft Kobbe, *Duke* 3925 (MO); vic of Hill C-6, Ft Sherman, shaded areas, *Duke* 4384 (MO); (Río) Chagres, *Fendler 55* (MO, US); Ancon Hill, *Greenman & Greenman 5106* (MO); Orchid I off Barro Colorado I, clearing at French Lock site, *Kenoyer 406* (US); Ancon Hill, dry hillsides, alt 100 m, *Killip 3019* (MO, US); betw Frijoles & Monte Lirio, along railroad, alt 30 m, *Killip 12122* (US); top of bluff above gulf, *McDaniel 5177* (MO); Balboa, *Mell* 5 (MO); Ancon, *Bro. Paul 159* (US); nr Old Ft San Lorenzo, mouth of Río Chagres, *Piper 5933* (US); vic of Ancon, *Piper 6001* (US); W slope of Ancon Hill, vic of Balboa, *Seibert 110* (GH, MO, NY); Barro Colorado I, Gross Pt., *Shattuck 943* (MO); Balboa, moist thicket, *Standley 25567* (US), wet open bank, *Standley 25590* (US), weed in garden, *Standley 26110* (US), in cornfield, *Standley 29305* (US); hills W of Canal, nr Gatun, *Standley 27300* (US); Gamboa, brushy slope, *Standley 28372* (US); vic of Summit, brushy slope, *Standley 30079* (US); vic of Ft Sherman, *Standley 30923* (US); Darien Station, open bank, *Standley 31564* (US); vic of Río Cocolí, Rd K-9, along roadside, *Stern et al. 40* (MO, US). CHIRIQUI: Boquete, alt 3800 ft, *Davidson 594* (F, GH, MO, US); El Boquete, roadside, alt 2300 m, *Killip 3503* (US); vic Boquete, from Boquete to 3 miles N, second growth, cultivated areas & roadsides, alt 3300-4200 ft, *Lewis et al. 330* (MO), *344* (MO); vic of El Boquete, alt 1000-1300 m, *Maxon 4929* (US), brushy pasture, *Maxon 5114* (US); pastures around El Boquete, alt 1000-1300 m, *Pittier 2892* (US); vic of Boquete, alt 1200-1500 m, *Woodson & Schery 720* (GH, MO). COCLE: El Valle, ca 3.1 km from El Greco Hotel, along rd, *Correa & Dressler 1010*

(MO); 12 mi NE of Penonomé, granitic river gorge, alt 1200 ft, *Lewis et al. 1508* (MO); hills NE of El Valle de Antón, disturbed forest edges, alt 2000 ft, *Lewis et al. 1808* (MO); El Valle de Antón, edge of cloud forest & roadside, 1000-2000 ft, *Lewis et al. 2545* (MO); at foot of Cerro Pilón, cloud forest, alt ca 2000 ft, *Dwyer & Correa 7986* (MO); above Penonomé, *Williams 277* (NY, US); betw Las Margaritas & El Valle, *Woodson et al. 1240* (GH, MO, NY, US), *1747* (GH, MO). COLON: María Chiquita, along shore above beach, *Ebinger 444* (MO); 2.4 mi SW of Piña, rain forest by beach & rd, *Lewis et al. 1846* (MO); betw Río Piedras & Puerto Pilón, roadside, *Lewis et al. 3214* (MO); vic of Palenque, nr sea level, *Pittier 4131* (US). DARIEN: village of Mannene, *Kirkbride & Bristan 1596* (MO). HERRERA: 10 mi S of Ocú on Las Minas Rd, *Graham 246* (GH). PANAMA: vic of provincial boundary, along rd between Las Uvas, Province of Panama, and El Valle, Coclé Province, *Bartlett & Lasser 16664a* (MO), 5-6 mi E of Chepo on PanAmerican Hwy, *Duke 4022* (GH, MO); Río Chagres, 1 mi above Madden Lake, *Duke 4478* (MO); PanAmerican Hwy at Río Mamoni, ca 4 mi beyond Chepo, *Duke 5565* (GH, MO); Cerro Azul, *Duke 9366* (MO); Alhajuela, river bank, *Bro. Heriberto 1* (US); 2-3 mi S of Goofy Lake, rd to Cerro Jefe, lower elev of cloud forest, alt 2000-2200 ft, *Lewis et al. 239* (MO); tributary of Río Chagres, 5 mi SW of Cerro Brewster, sandy & rocky river banks, alt ca 1000 ft, *Lewis et al. 3506* (MO); Cerro Campana, common along roadside nr moist woods, alt 2900 ft, *McDaniel 6873* (MO); banks of Mamoni River, above Chepo, alt 20-25 m, *Pittier 4727* (US). SAN BLAS: airport at Irandí, *Duke 6505* (GH, MO); mainland opposite Ailigandí, from mouth of Río Ailigandí to 2.5 mi inland, marshy rain forest, often native plantations, *Lewis et al. 64* (MO). PROVINCE UNKNOWN: s. loc., *Moore 42* (F); western Panama, *Stork s.n.* July-Aug 1923 (US).

6. **Polygala hygrophila** H.B.K., Nov. Gen. Sp. Pl. **5:** 395, 1823.

Slender, erect *annuals,* simple or slightly branched, 7-50 cm high; stems wing-angled, glabrous. *Leaves* subverticillate at the base of the stem, the others alternate, linear to linear-lanceolate, mucronate or acute apically, cuneate basally, 1-nerved, the margins slightly revolute, glabrous, 6-12 mm long, 0.5-1.2 mm wide, sessile. *Racemes* very dense, cylindric or cylindric-ovoid, slightly comose apically, 1-2.6 cm long, 6.5-12 mm wide, the peduncle to 5 cm long; bracts linear-lanceolate, acuminate-subulate, usually carinate, ciliolate basally, glabrescent toward the apex, 2-3 mm long. *Flowers* white or greenish-white, tinted pink or lavender, subsessile; sepals elliptic-oblong to ovate, subacute, occasionally with a ridge along the costa on the dorsal side, then usually appearing carinate, 1.7-2.2 mm long; wings oval, sometimes suborbicular, rounded apically, cuneate-rounded basally, sometimes with a ridge along the costa on the dorsal side, then usually appearing concave, 5-7-nerved, 4.3-5 mm long, 3-3.8 mm wide; upper petals oval or obovate-oblong, rounded apically, ca equaling the keel; keel 2.5-3 mm long, the crest irregularly trilobate on each side; staminal tube glabrous inside, the filaments 0.4-0.6 mm long; ovary ovoid to orbicular, 0.5-1.3 mm long, 0.4-0.7 mm wide, the style ascendent, 0.5-1 mm long, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose, sessile stigma. *Capsules* suborbicular, 1.5-1.9 mm long, 1.4-1.9 mm wide; seeds (Fig. 1e) ellipsoid, 1.7-1.9 mm long, sparsely short-pubescent; aril corneous above, the 2 lobes narrowly and obliquely oblong, appressed, 0.9-1.6 mm long, glabrous.

British Honduras, Costa Rica, Panama and Santo Domingo; northern South America.

CANAL ZONE: Río Azote Caballo, savannas along drowned river, alt 66-70 m, *Dodge et al. 16854* (MO); Sabana de Marcelito, nr El Vigía, *Pittier 2384* (US). CHIRIQUI: nr

El Boquete, pastures, alt 1000-1300 m, *Pittier* 2893 (US); Sabana de la Tortuga, betw El Boquete & Caldera, after fire, alt 300-700 m, *Pittier* 3317 (US); Cerro Vaca, alt 900 1136 m, *Pittier* 5347 (F, US); Jaremillo, Boquete, alt 4500 ft, *Terry 1274* (F, GH, MO, US); vic of Boquete, alt 1200-1500 m, *Woodson & Schery 780* (MO). COCLE: Penonomé, level ground outside town, *Ebinger 1013* (MO); Aguadulce, savannas nr sea level, *Pittier 4876* (GH, NY, US); Picacho de Olá, alt 350 600 m, *Pittier* 5058 (US). PANAMA: Casa Larga, dry savannas, alt 65 m, *Allen 2971* (GH, MO, US); hills NE of Hacienda La Joya, alt 50-300 m, *Dodge et al. 16877* (MO); nr Rio Pacora & Chepo hwy, savanna, *Duke 5914* (MO); Juan Díaz, dry fields, alt 50 m, *Killip 3267* (MO, US); SE slope of Cerro Campana, roadside & grassland, *Lewis et al. 3115* (MO); Cerro Campana, common in bog in grassland, alt 2400 ft, *McDaniel 6921* (MO); Sabana de Dormisolo, nr Chepo, alt 60-80 m, *Pittier 4651* (US).

7. **Polygala longicaulis** H.B.K., Nov. Gen. Sp. Pl. **5:** 396, 1823.

Slender erect *annuals,* simple or sparsely branched, 6-60 cm high; stems glabrous. *Leaves* alternate, linear or linear-lanceolate, sometimes with a whorl of 3 reduced narrow-obovate leaves at base of stem, acute or cuspidate apically, acute or attenuate basally, 1-nerved, the margin slightly revolute, glabrous, punctate, 4-28 mm long, 0.5-3 mm wide, subsessile. *Racemes* depressed-subglobose or globose, densely flowered, 6-12 mm long, 6-18 mm wide, the axis to 3.5 cm long, the peduncle to 12 cm long; bracts lance-ovate, subulate, the margins glandular-ciliate, usually gland-dotted on back, 0.8-1.2 mm long. *Flowers* varying from white to deep purple, the pedicels 1.5-3 mm long; largest sepal ovate or elliptic, cuspidate, 5-nerved, 1.7-2.2 mm long, the smaller 2 ovate, occasionally elliptic, cuspidate, gland-dotted basally, 1.6-1.9 mm long; wings elliptic, obong or ovate-oblong, cuspidate apically, usually cuneate-rounded basally, 3-nerved, bearing a few glands on back, 4.7-5.8 mm long, 1.5-2 mm wide; upper petals suboblong to nearly obovate, obtuse, 3.6-5.3 mm long; keel 3-4.3 mm long, gland-dotted apically and basally, the crest lobed, the lobes 0.6-1 mm long, usually 6, rarely 8, single or irregularly forked; staminal tube glabrous inside, the filaments very short; ovary oblong, 1-1.4 mm long, 0.7-0.9 mm wide, the style slender, straight, 1.8-2.2 mm long, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose, papillose stigma supported on a minute stalk. *Capsules* ovoid-oblong, bearing a double line of glands along the septum, 2.8-4 mm long, 1.4-2.2 mm wide; seeds (Fig. 1h) conic, sericeous, comose basally, 1.8-2.5 mm long (including the coma); aril minute or absent.

Mexico through Central America and the West Indies to Argentina; frequent in Panama.

CANAL ZONE: nr BOQ, Ft Kobbe, *Duke 3912* (MO); summit of Ancon Hill, dry hillsides, *Killip 3021* (GH, NY, US); open grassy slope, common, *Standley 25217* (US). CHIRIQUI: W of Gualaca, level ground, common, alt 500 ft, *Allen 5052* (MO); El Valle, ca 3.6 m from El Greco Hotel along rd to InterAmerican Hwy, *Correa & Dressler 1008* (MO); David airport, disturbed grassland, edge of marsh, alt 25 ft, *Lewis et al. 768* (MO). COCLE: Nata, alt ca 50 m, *Allen 825* (GH, MO, NY, US); Llano Bonito, N of Las Margaritas, alt 400-500 m, *Seibert 522* (GH, MO, NY); betw Las Margaritas & El Valle, *Woodson et al. 1266* (GH, MO, NY, US), *1274* (GH, MO). PANAMA: vic of provincial boundary, along rd betw Las Uvas (Panama) and El Valle (Coclé), *Bartlett & Lasser 16665* (MO); Taboga I, alt 900 ft, *Colleustte 475* (US); nr beach at Nueva Gorgona, *Duke 4543* (MO); rd toward top of Cerro Campana, bald savanna-like areas, *Duke 5951* (MO); nr Chepo, savannas, *Duke 6038* (MO); Tocumen airport, *Dwyer*

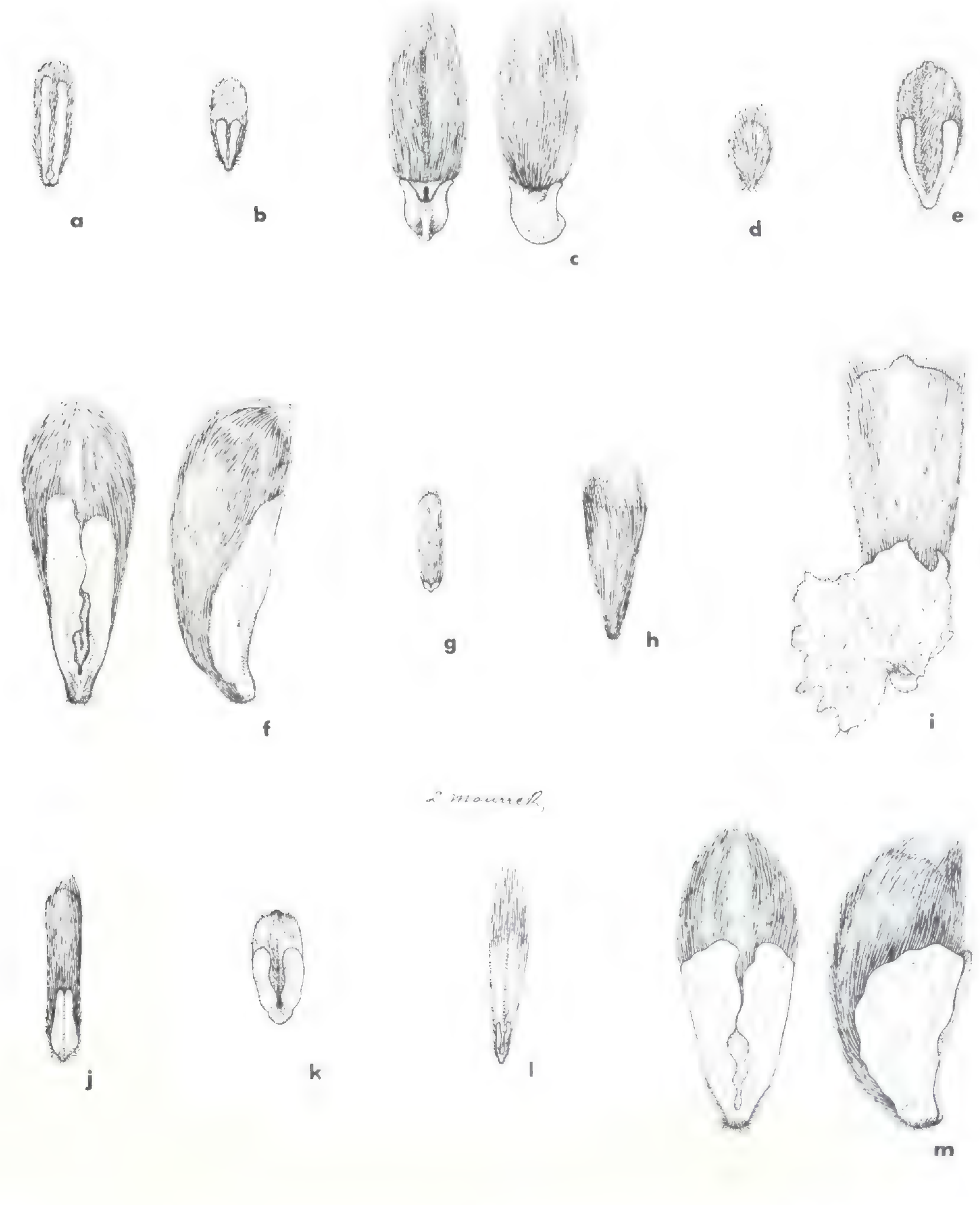

Fig. 1. Seeds of *Polygala* species. A, *P. aparinoides* Hook. & Arn.; B, *P. asperuloides* H.B.K.; C, *P. brizoides* St.-Hil.; D, *P. fendleri* var. *heterothrix* Blake; E, *P. hygrophila* H.B.K.; F, *P. jefensis* W. H. Lewis; G, *P. leptocaulis* Torrey & Gray; H, *P. longicaulis* H.B.K.; I, *P. panamensis* Chodat; J, *P. paniculata* L.; K, *P. timoutou* Aublet; L, *P. variabilis* H.B.K.; M, *P. wurdackiana* W. H. Lewis. All × 10.

2575 (MO); nr Ríomar, open pasture land, *Ebinger 505* (MO); Cerro Campana, grassland, *Ebinger 930* (MO); San José I, East Harbor, rocky coastal bluffs, *Erlanson 445* (GH, US), vic of South Beach, rocky coastal bluffs, *Erlanson 527* (GH, US); San José I, East Harbor, on bald spots reaching greater height than surrounding grasses, *Harlow 22* (GH, US); Tumba Muerto, *Bro. Heriberto 170* (US); San José I, East Bay, rocky open place at head of sea cliffs, *Johnston 193* (GH, MO, US); Taboga I, dry fields, 200 m, *Killip 3189* (MO, US); (Las) Sabanas, *Bro. Paul 15* (US); Chepo, alt 60 m, *Pittier s.n.*, Oct 1911 (US); Laguna de Portala, nr Chepo, alt 50 m, *Pittier 4572* (US); Las Sabanas, open grassy slope, common, *Standley 25912* (US); nr Punta Paitilla, savanna, common, *Standley 26294* (US); E of Pacora, wet savanna, alt ca 25 m, *Woodson et al. 754* (MO). VERAGUAS: 2 mi W of Santiago on PanAmerican Hwy, common along banks of hwy, *Duyer et al. 7549* (MO).

8. **Polygala variabilis** H.B.K., Nov. Gen. Sp. Pl. **5:** 397, 1823.

Slender erect *annuals,* simple or sparsely branched, 14-20 cm high; stems ribbed, glabrous. *Leaves* all alternate, linear, acute or acuminate, 1-nerved, glabrous, usually punctate, 3-9 mm long, 0.3-0.8 mm wide, subsessile. *Racemes* somewhat dense, conic, to 1 cm long and to 7 mm wide, the axis to 3 cm long. *Flowers* purple, the pedicels 0.5-0.8 mm long; largest sepal ovate, obtuse or blunt, 1.5-1.9 mm long, sometimes with a few basal glands; the smaller 2 ovate to suboblong, obtuse, 1-1.4 mm long, gland-dotted along the costa; wings elliptic to oblong, rounded or rarely bluntly mucronate apically, cuneate basally, 3-nerved, bearing a few glands basally and rarely along the costa, 2.6-3.2 mm long, 2.5-3.4 mm wide; upper petals ovate-lanceolate, obtuse, ca equaling the keel; keel 2.5-3.4 mm long, gland-dotted apically and basally, the crest lobed, the lobes 6 or 8, 0.5-0.8 mm long; staminal tube glabrous inside, the filaments very short; ovary oblong, 0.5-0.8 mm long, 0.1-0.2 mm wide, the style straight, 0.3-0.4 mm long, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose stigma supported on a minute stalk. *Capsules* ovoid-oblong, 3 mm long, 1.2-1.6 mm wide; seeds (Fig. 11) conical, sericeous, comose basally, 2.5-2.7 mm long (including the coma), the 2 lobes of the aril narrowly oblong, appressed, 0.5 mm long, glabrous.

Southern Mexico to northern South America (Amazon basin) and Trinidad; rare in Panama.

COCLE: Aguadulce, savannas nr sea level, *Pittier 4875* (US).

This species is closely related to *P. longicaulis* H.B.K.

9. **Polygala timoutou** Aublet, Hist. Pl. Gui. Fr. 737, 1775.

Slender erect *annuals,* simple or slightly branched, 8-18 cm high; stems wing-angled, glabrous. *Leaves* nearly all in whorls of 3, occasionally the uppermost opposite or alternate, oval to obovate, mucronate at the acutish apex, cuneate basally, 1-nerved, glabrous, 4-16 mm long, 3-5 mm wide, sessile or subsessile. *Racemes* cylindric, very dense, slightly comose apically, 1-4 cm long, 8-11 mm wide, the peduncle very short, to 12 mm long; bracts linear-lanceolate, subulate, 2-3 mm long. *Flowers* pink, subsessile; sepals lanceolate, acuminate, 1.5-2.4 mm long; wings oval to suborbicular, mucronate at the rounded apex, cuneate-rounded basally, ca 3-nerved, 3-4.6 mm long, 1.8-3.2 mm wide; upper petals oblong to obovate-oblong, rounded apically, ca equaling the keel; keel 1.8-2 mm long, the

crest 6-9-lobed, the lobes 0.3-0.6 mm long; staminal tube glabrous inside, the filaments 0.4-0.8 mm long; ovary ovoid to almost orbicular, 0.5-0.9 mm long, 0.4-0.6 mm wide, the style ascendent, 0.4-0.6 mm long, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose, sessile stigma. *Capsules* orbicular to orbicular-ovoid, 1.2-1.4 mm long, 1-1.2 mm wide; seeds (Fig. 1k) ellipsoid, 1.2-1.3 mm long, sparsely short-pubescent; aril corneous above, the 2 lobes narrowly oblong, appressed, 0.6-0.9 mm long.

British Honduras, Costa Rica and Panama; Trinidad and northern South America to the Amazon delta.

CANAL ZONE: along drowned Río Azote Caballo, alt 66-70 m, *Dodge et al. 16855* (MO); Sabana de Marcelito, nr El Vigía, *Pittier* 2385 (US). PANAMA: Casa Larga, dry savannas, alt 65 m, *Allen* 2972 (MO).

10. **Polygala aparinoides** Hook. & Arn., Bot. Beech. Voy. 227, 1836.

Erect or spreading, simple or branched slender *perennials,* 5-27 cm high; stems winged, glabrous. *Leaves* verticillate, in whorls of 3-5, obovate to elliptic-obovate, sometimes the uppermost lanceolate to elliptic-lanceolate, 7-21 mm long, 4-8 mm wide, cuspidate apically, attenuate basally, 1-nerved, the margin denticulate, glabrous, glandular-punctate; petioles ca 1 mm long. *Racemes* cylindric, acuminate, rather dense, 4-20 mm long, 4-6 mm wide, the axis to 3.5 cm long; bracts deciduous, lanceolate, acuminate, glabrous, 0.6-0.8 mm long. *Flowers* purple or greenish-purple, the pedicels 0.4-0.7 mm long, outer sepals often marginally ciliate from the apex to the middle, glabrous toward the base, usually gland-dotted, the largest ovate, obtuse, 1-1.2 mm long, the smaller 2 oblong to oblong-ovate, often somewhat acute, otherwise obtuse, 0.7-1 mm long; wings obovate to elliptic-obovate, rounded apically, short-clawed basally, glabrous, usually gland-dotted, 1.6-2 mm long, 1.1-1.2 mm wide; upper petals 1.9-2.2 mm long, ovate to rhombic-ovate, obtuse or rounded; keel 1.4-1.6 mm long, the crest 4-6-lobed, the lobes 0.3-0.7 mm long; staminal tube often split ca halfway into 2 bundles, each of 4 short filaments; ovary oblong to ovoid, 0.4-0.6 mm long, 0.3-0.5 mm wide, the style ascending, 0.2-0.3 mm long, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose, sessile stigma. *Capsules* broadly ellipsoid, 1.7-2.2 mm long, 1.4-1.9 mm wide; seeds (Fig. 1a) oblong, 1.4-1.8 mm long, appressed-pilose, often equaled by the 2 narrowly oblong, appressed lobes of the aril.

Mexico (Jalisco), Guatemala, British Honduras and Panama.

CHIRIQUI: Boquete, alt 3800 ft, swamp in potrero, *Davidson 574* (MO, US); El Boquete, alt 1300 m, *Killip 3500* (US); 12.4 mi N of David, edge of steep river bank, *Lewis et al. 721* (MO); vic of Boquete, alt 1200-1500 m, *Woodson & Schery 779* (MO), 785 (MO).

Closely allied to *P. asperuloides* H.B.K.

11. **Polygala asperuloides** H.B.K., Nov. Gen. Sp. Pl. **5:** 403, 1823.

Erect or spreading, simple or branched slender *annuals,* 5-13 cm high; stems winged, glabrous. *Leaves* verticillate, often in whorls of 4-5, the uppermost some-

times in 2's or 3's, lanceolate or lance-elliptic, 7-9 mm long, 2.7-7 mm wide, the lowermost usually ovate or orbicular-obovate, 7-9 mm long, 4.5-5 mm wide, cuspidate apically, attenuate basally, 1-nerved, the margins entire or rarely remotely crenate, glabrous, glandular-punctate; petioles less than 1 mm long. *Racemes* cylindric, loosely flowered, 4-22 mm long, 4-6 mm wide, the axis to 3.5 cm long; bracts deciduous, lanceolate, subulate, glabrous, 0.5-0.7 mm long. *Flowers* purple, the pedicels 0.4-0.7 mm long; outer sepals sometimes ciliolate, with 2 large glands on the back, the largest sepal ovate to orbicular-ovate, obtuse, 1-2 mm long, the smaller 2 oblong, obtuse, 0.7-0.9 mm long; wings elliptic to obovate, rounded apically, cuneate basally, glabrous, gland-dotted, 1.6-1.8 mm long, 1 mm wide; upper petals 1.8-2 mm long, triangular-ovate to rhombic-ovate, obtuse; keel 1.4-1.6 mm long with 2 large glands apically, the crest 6-lobed, the lobes 0.4-0.7 mm long; staminal tube glabrous inside, the filaments 0.1-0.3 mm long; ovary oblong or ovoid, 0.3-0.5 mm long, 0.3-0.4 mm wide, gland-dotted, the style ascending, 0.2-0.3 mm long, developed distally into a navicular cavity, the apical end of which has a tuft of hairs, the inner end a globose, sessile stigma. *Capsules* broadly ellipsoid, 1.2-1.4 mm long, 1-1.2 mm wide, gland-dotted; seeds (Fig. 1b) oblong, 1-1.2 mm long, appressed-pilose; aril with the 2 lobes oblong, appressed, 0.5-0.7 mm long.

Guatemala, British Honduras and Panama; also in Colombia and Venezuela.

COCLE: vic of El Valle, alt 800-1000 m, *Allen* 773 (MO, US); vic of El Valle de Antón, alt 800 m, *Allen 1932* (MO, US); Llano Bonito, N of Las Margaritas, open llanos, alt 400-500 m, *Seibert* 523 (MO, US). PANAMA: along rd toward top of Cerro Campana, bald savanna-like areas, *Duke* 5950 (MO); Cerro Campana, grassland, *Ebinger* 920 (MO).

12. **Polygala wurdackiana** W.H.Lewis, Ann. Missouri Bot. Gard. **55:** 365, *fig. 1,* 1969.

Suffrutescent *perennials* to 1.3 m, branched above, often with 2-4 branchlets at a node, glabrous, angular, green. *Leaves* (2-)3-5 in whorls; petioles 4-10 mm long, glabrous; blades elliptic to less commonly ovate, basally somewhat attenuated, apically acute, the margins remotely crenate, glabrous, sparingly punctate, 4-7.5 cm long and 1.8-3 cm wide decreasing in size apically. *Racemes* glabrous, the axis elongating to ca 9 cm, the flowers loose; bracts ovate, glabrous, deciduous, 0.8-1 mm long. *Flowers* white, the pedicels to 3 mm long; outer sepals marginally ciliate, the largest ovate, concave, 2.3-2.5 mm long, the smaller 2 ovate to oblong and usually short-connate basally, sometimes free, 1-1.5 mm long; wings obovate to oblong-elliptic, apically rounded, basally short-clawed, marginally ciliate, persistent, 3.2-3.8 mm long; petals with upper pair obovate, rounded, equaling the keel; keel 2.5-2.8 mm long with a crest 8-22-lobed (often irregularly forked and varying in size). *Capsules* widely oblong, glabrous, 4-5 mm long, 3.2-4 mm wide; seeds ovate, 4 mm long, densely pubescent with hairs copper colored at maturity; arils 2.5-3 mm long, the 2 lobes broadly obovate, appressed.

Apparently endemic to the cloud forest above 2500 ft in the vicinity of El Valle de Antón, Panama.

COCLE: Cerro Pajita, hills N of El Valle de Antón, 1000-1200 m, common, *Allen & Allen 4170* (MO); Cerro Caracoral (vic of El Valle de Antón), elfin forest, alt ca 1000 m, *Duke & Dwyer 15101* (MO, NY); mountains N of El Valle de Antón, cloud forest, alt 2500-3000 ft, *Lewis et al. 1723* (holotype MO; isotypes DUKE, K, UC, US).

13. **Polygala jefensis** W.H. Lewis, Ann. Missouri Bot. Gard. **55:** 367, 1969.

Herb to shrub 2 m high (*Duke 9431*), branched above with 2-3 branchlets per node, glabrous, angular. *Leaves* 4-5 in whorls; petioles usually 4-7 mm long, glabrous; blades elliptic, somewhat attenuated basally, acuminate apically, the margins remotely crenate, glabrous, densely punctate, the more mature 4-5.5 cm long and 2-2.5 cm wide. *Racemes* terminal, glabrous, the axis to 7 cm long, the flowers ± loose; bracts ovate-lanceolate, ciliate, deciduous, 0.8-1 mm long. *Flowers* greenish-white, the pedicels to 2 mm long; outer sepals marginally ciliate, the largest ovate, concave, 2 mm long, the smaller 2 ovate to oblong, 1 mm long, usually shortly connate basally, each with 2 large glands; wings broadly obovate, apically rounded, basally short-clawed, marginally ciliate, persistent, 3.5 mm long, 2.5 mm wide; petals with upper pair obovate, rounded, 3 mm long, glabrous; keel 3 mm long with a crest 6-20-lobed (mostly 6). *Capsules* widely oblong to subglobose, glabrous, 4 mm long, 3-3.5 mm wide; seeds ovate, curved, 4 mm long, pubescent with hairs copper colored at maturity; arils 2.8-3 mm long, the 2 lobes oblong, appressed.

Endemic to Cerro Jefe, Province of Panama; closely allied to *P. wurdackiana*.

PANAMA: Cerro Jefe, alt 3400 ft, *Bouché s.n.* (holotype MO), *Duke 9431* (MO), alt 2700-3000 ft, *Tyson et al. 4397* (MO).

2. SECURIDACA

Securidaca L., Syst. Nat. ed. 10, 1155, 1759, nom. cons., non L. (Sp. Pl. ed. 1, 707, 1753).

Elsota Adanson, Fam. **2:** 358, 1763.

Woody *vines*, usually scandent shrubs, or trees. *Leaves* alternate, entire, short-petioled, generally with corneous peziziform stipular glands. *Racemes* terminal or axillary, often paniculate. *Flowers* usually pink or purple; sepals 5, free, the outer 3 herbaceous, the inner 2 (wings) much larger, petal-like; petals 3, the lowest (keel) boat-shaped, clawed, with a plicate, fimbriate crest, the 2 upper adnate to the base of the staminal tube but distinct from the keel; stamens 8, their filaments connate nearly to the apex into a sheath split on the upper side, adnate to the keel and upper petals toward the base; anthers confluently 1-celled, opening by a large introrse-apical pore; ovary unilocular through the abortion of the second locule, with an appendage on one side which develops into the wing of the fruit, the style sickle-shaped, excavated apically, the stigma 2-lobed, approximate, the ovule solitary, pendulous; disc a low fleshy ring at base of the ovary. *Fruit* a samara, the wing large, 1-seeded; seed glabrous, exarillate, endosperm wanting, the cotyledons thick-fleshy, oily.

Perhaps 50 species in the tropics and subtropics excluding Australia; two species occur in Panama.

a. Leaves acute or obtuse apically, rounded or cuneate basally, puberulent, strigose, or glabrescent beneath; flowers small; largest sepal from the outer whorl 3-4 mm long, the smaller two ca 2 mm long; wings glabrous on the outside; upper petals 5-7 mm long; keel with a wide many-plicate crest, 1-1.8 mm long . . . . . 1. *S. diversifolia*

aa. Leaves obtuse to rounded or sometimes emarginate apically, broadly rounded or truncate basally, softly and densely velvety-pilose beneath; flowers large; largest sepal from the outer whorl 3.5-5 mm long, the smaller two 2.6-4 mm long; wings pubescent on the outside; petals 8-11 mm long; keel with a narrow few-plicate crest less than 1 mm long, sometimes obsolete . . . . . 2. *S. tenuifolia*

1. **Securidaca diversifolia** (L.) Blake in Standley, Contr. U. S. Nat. Herb. **23**: 594, 1923.

Polygala diversifolia L., Sp. Pl. 703, 1753.

Scandent *shrubs* or woody vines; branches terete, puberulous, strigose or glabrescent. *Leaves* elliptic-oblong or oblong-ovate to broadly ovate or oval, acute or obtuse apically, rounded or cuneate basally, 3.5-8.5 cm long, 1.5-5 cm wide (leaves of the flowering branches much smaller, usually oval or suborbicular), pergamaceous or chartaceous with veins densely reticulate and prominulous on both sides, somewhat shining, puberulent or glabrous above, puberulent, strigose or glabrescent beneath, usually more densely so along the veins; petioles strigose or puberulous, 2-7 mm long. *Racemes* loose or rather dense, terminal or axillary, sometimes branched, 1.5-8 cm long, 1.8-2.5 cm wide; peduncles 2 cm or less, the axis to 6 cm long, densely strigose or puberulous; bracts lanceolate to ovate, acuminate, pubescent, sometimes persistent, 1.5-3 mm long. *Flowers* pink or purple, the pedicels 3-7 mm long, pubescent; outer sepals oval, rounded, puberulent except near the ciliate margin, the largest usually concave, 3-4 mm long, the smaller 2 ca 2 mm long; wings suborbicular to oval or ovate, broadly rounded apically, usually emarginate, short-clawed basally, usually unequal, the margin sometimes ciliate, the outside glabrous (including the claw), 7-10 mm long, 6-8 mm wide; upper petals subspatulate, truncate apically, usually sparsely puberulent basally inside, rarely ciliate on the margin, 5-7 mm long; keel 7.5-10 mm long, as folded together 1.9-2.8 mm wide, the middle portion of the apex forming a wide, many-plicate, irregularly toothed or fimbriate crest, 1-1.8 mm long, the keel frequently ciliate on the margin, sometimes the basal half sparsely puberulous on the outside or glabrous, usually puberulous inside on the saccate portion; basal half of staminal sheath pubescent, the free part of the filaments 2.5-3.2 mm long; ovary compressed-ellipsoidal, glabrous, 0.8-1 mm long, 0.6-0.8 mm wide, slightly margined on one side, the appendage on the other side ovate, acute, densely puberulent, extending beyond the ovary, 7-9 mm long, the style 9-11 mm long, the stigma 2-lobed, approximate. *Samara* (not seen at maturity) greenish or straw-colored, puberulous, 4-6 cm long, fruiting locule plump, elevated-reticulate, 5-8 mm long, margined on upper side, the margin 1-2.5 mm wide, prolonged beyond the fruiting locule and connate with the wing, usually with a triangular free tooth apically; wing obovate, narrower basally, 3.2-5 cm long, 3-4 mm wide (excluding the connate upper wing-margin of fruiting locule), 11-17 mm near middle (after Blake, N. Amer. Fl. **25**: 373, 1924).

Mexico to Peru and the Lesser Antilles.

BOCAS DEL TORO: Changuinola Valley, *Dunlap* 577 (F, US). CANAL ZONE: Barro Colorado I, shoreline SW of Fairchild Point, *Croat* 4865 (MO), 4873 (MO); vic of former town of Empire, Culebra Cut & vic, alt 80 m, *Hunter & Allen* 772 (GH, MO); Gamboa Rd, *Jones* 311 (US), 312 (US); s. loc. *Joseph* 462 (MO); Ancon, hospital grounds, alt 20-80 m, *Mason* 4 (F, GH, NY, US); Red Tank to Pueblo Nuevo, Chiva-Chiva Trail, *Piper* 5126 (F, GH, NY, US); Barro Colorado I, *Shattuck* 798 (F, MO), 834 (MO); Ancon Hill, moist thicket, *Standley* 26327 (US); nr Ft Randolph, *Standley* 28670 (US); Balboa, *Standley* 29266 (US); betw France Field & Cativa1, *Standley* 30387 (US); Obispo, *Standley* 31747 (US); rd from Ft Sherman to Ft San Lorenzo, *Tyson & Blum* 3757 (MO), 3758 (MO); nr Miraflores, *White* 77 (GH, MO); Barro Colorado I, *Woodward & Vestal* 335 (A, F, GH, MO), 453 (A, F, GH, MO), 556 (F, GH, MO), 618 (A, F, GH, MO); Ancon, hospital, *Zetek Z-2526* (F). COCLE: vic of El Valle, alt 600-1000 m, *Allen 1634* (GH, MO, NY, US); mountains beyond La Pintada, alt 400-600 m, *Hunter & Allen* 543 (MO); Penonomé & vic, *Williams 110* (NY), 138 (NY), 411 (NY), 412 (NY). LOS SANTOS: Bahía Honda, *Elmore H17* (F). PANAMA: "La Victoria," vic of La Joya, alt 200 m, *Allen 4317* (MO); San Jose I, *Campbell 9* (GH); 2 mi S of Cerro Azul, alt ca 700 ft, *Dwyer* 3531 (MO); summit of Cerro Campana, rain forest, *Dwyer et al.* 4831 (MO); San José I, *Erlanson* 33 (GH, NY, US), *Johnston* 527 (GH), 572 (GH, MO, US), 903 (GH), 1067 (GH); Taboga I, forested slopes, *Macbride 2815* (US); Camino del Boticario, nr Chepo, alt 30-50 m, *Pittier* 4542 (F); vic of Juan Franco race track, nr Panama, moist thicket, *Standley* 27725 (US).

Securidaca volubilis L., reported by Hemsely (Biol. Centr.-Amer. Bot. **1:** 63, 1879) from Panama (Lion-Hill railway station and Taboga I), is probably *S. diversifolia,* a misidentification which Oort (Rec. Trav. Bot. Néerl. **36:** 678, 1939) notes as having been frequent. Seemann's *S. pubescens* (Bot. Voy. Herald 80, 1852), collected near Panama (City), will probably prove to be *S. pubescens β ovata* DC. (Prodr. **1:** 341, 1824), and if so then it should also be included under *S. diversifolia* (see Oort, loc. cit. 680). Finally, *S. tomentosa* of Hemsley (loc. cit.), but not *S. tomentosa* St.-Hil. (Fl. Bras. Merid. **2:** 68, *t.* 96, 1829), collected near Panama City, may be included here though this is not certain.

2. **Securidaca tenuifolia** Chodat, Bull. Herb. Boissier **3:** 545, 1895.

Elsota chrysotricha Riley, Kew Bull. **1927:** 119, 1927.
E. tenuifolia (Chodat) Sandwith, Kew Bull. **1929:** 79, 1929.

Scandent *shrubs* or woody vines; branches terete, softly pilose. *Leaves* oval, oblong-ovate or ovate, obtuse to rounded, sometimes emarginate apically, broadly rounded or truncate basally, 3.5-9.5 cm long, 2-3.5(-4) cm wide, chartaceous, veins densely reticulate and prominulous on both sides, somewhat shining, sparsely pilose (usually more densely on margin) or glabrescent above, softly and densely velvety-pilose beneath, especially along the veins; petioles pilose, 2-4 mm long. *Racemes* loose or somewhat dense, terminal; peduncles 1 cm or less long, the axis 2.2-5 cm long, pilose; bracts lanceolate, acute to acuminate, pilose, deciduous, 1.8-2 mm long. *Flowers* pink; pedicels short-pilose, 5-8 mm long; outer sepals oval, rarely suborbicular, rounded, densely pilose on the outside except near the ciliate margin, the largest 3.5-5 mm long, the smaller two 2.6-4 mm long; wings suborbicular, broadly rounded apically, usually emarginate, short-clawed basally, the margin ciliate, the outside pubescent (including the claw), 9-12 mm long, 6-9 mm wide; upper petals obovate or obovate-spatulate, rounded,

usually undulate apically, attenuate and gibbous toward the base, glabrous, 8-11 mm long; keel 9.5-13 mm long, as folded together 5-6 mm wide, the apex forming a narrow, few-plicate, minutely toothed crest less than 1 mm long, sometimes obsolete, the keel ciliate on the margin, sometimes sparsely puberulent on the outside, puberulent inside on ca the basal half of the saccate portion; staminal sheath pubescent basally, the free portion of the filaments 2-2.8 mm long; ovary compressed-ellipsoidal, densely pubescent, 1.2-1.8 mm long, 0.8-1 mm wide, the style 7.5-11 mm long, the stigma 2-lobed, approximate. *Samara* densely short-pilose, 4.5-7 cm long, plump, elevated-reticulate, 7-11 mm long; wing obovate, narrower basally, 4-6 cm long, 14-22 mm wide near middle.

Panama and Trinidad.

CANAL ZONE: Curundú, Thunder Hill, *McDaniel 5186* (MO); Las Sabanas, *Pittier 6642* (US); betw Ft Clayton & Corozal, along old Las Cruces Trail, moist thicket, *Standley 29109* (US); vic of Río Cocolí, Rd K-9, *Stern et al. 301* (MO); Corozal, *Stevens 114* (US); Barro Colorado I, *Woodward & Vestal 505* (A, MO). COLON: Santa Rita Ridge, logging rd 19 km from Transisthmian Hwy, *Dwyer 8576* (MO). DARIEN: nr Punta Garachine, thorn forest, *Duke 1074* (US); vic of El Real, Río Tuira, edge of rd on Don Pablo Othon's farm, *Stern et al. 800* (GH, MO, US). PANAMA: vic of El Llano, *Duke 5512* (GH, MO); nr Río Tapia Juan Díaz region, roadside thicket, *Maxon & Harvey 6749* (GH, NY, US); Camino del Boticario, nr Chepo, alt 30-50 m, *Pittier 4542* (US); Old Panama, *Riley 148* (type of *Elsota chrysotricha;* MO, US); betw Matías Hernández & Juan Díaz, *Standley 32034* (US). VERAGUAS: along hwy nr Río Tabasara, *Woodson et al. 466* (MO). PROVINCE UNKNOWN: s. loc., *Grisebach s.n.* in 1857 (MO).

Our specimens of *S. tenuifolia* had been misidentified as *S. coriacea* Bonpl.

3. MONNINA

Monnina Ruiz & Pavon, Syst. Veg. Fl. Peru. Chile. 169, 1798.

Herbs, shrubs, or small trees. *Leaves* alternate, entire, short-petiolate, stipulate or with stipular glands. *Flowers* purple or blue; sepals 5, the outer 3 herbaceous, free, the inner 2 (wings) much larger, petaloid, and ± concave; petals 3, the lower (keel) not clawed, unappendaged, essentially free, the upper 2 spatulate, adnate below to the staminal sheath; stamens 8, very rarely 6, their filaments connate nearly to apex into a sheath split on the upper side, the anthers confluently 1-celled, opening by a large introrse-apical pore; ovary 1-locular, the style geniculate, the stigma with 2 dissimilar lobes with the outer (lower) ± acute and the inner (upper) tubercled, the ovule 1, pendulous; disc reduced to a gland at base of the ovary. *Drupe* with a fleshy coat, the surface rugose, marginate, 1-seeded; seeds glabrous, exarillate, the cotyledons thick.

About 150 species from the southern U.S. and Mexico to Argentina and Chile; predominantly northwestern South American. A comprehensive treatment of the genus is needed and will ultimately be provided by Ferreyra (for Peru see Jour. Arnold Arb. **27:** 123-167, 1946; for Ecuador see Lloydia **16:** 193-226, 1953; for Colombia see Smithsonian Misc. Coll. **121:** 1-59, 1953; for Venezuela see Brittonia **9:** 9-18, 1957). Two species are recognized for Panama.

a. Racemes slightly comose toward the apex; bracts lance-subulate, 4.5-5 mm long; leaves elliptic to oval, cuneate-attenuate or obtuse basally, 6-13 cm long, 2.5-7 cm wide; lower sepals of the outer whorl without a lateral lobe . . . . . 1. *M. sylvatica*

aa. Racemes not at all comose; bracts triangular-ovate, acute or obtuse, 1.4-2.2 mm long; leaves oblanceolate to obovate-elliptic, acute to acuminate basally, 3-10 cm long, 1-3.5 cm wide; lower sepals of the outer whorl usually with a small lateral lobe ..... 2. *M. xalapensis*

1. **Monnina sylvatica** Schlecht. & Cham., Linnaea **5**: 231, 1830.—Fig. 2.

M. crispata Blake, N. Amer. Fl. **25**: 377, 1924.

Shrubs or herbs to 3 m high; branches striate, incurved-puberulous or glabrous. *Leaves* elliptic, elliptic-ovate, or oval, acute or acuminate apically, cuneate to cuneate-attenuate or obtuse basally, 6-13 cm long, 2.5-7 cm wide, usually glabrous, sometimes pubescent on both sides, the costa prominulous beneath with 4-6 pairs of conspicuous lateral veins; petioles 3-7 mm long, glabrous or pubescent. *Racemes* cylindric, somewhat dense, obtuse, slightly comose toward the apex, to 9 cm long, 8-18 mm wide; peduncles to 5.5 cm long, several or numerous, simple or branched, terminal or axillary, the axis to 16 cm long, pubescent; bracts lance-subulate, attenuate, ciliate, deciduous, 4.5-5 mm long. *Flowers* purple or blue; pedicels 1-2 mm long, pubescent; outer sepals ovate to oblong-ovate, obtuse, rarely acute, ciliate on the margins, sometimes short-pubescent or glabrescent on the outside, the largest 2.5-3 mm long, sometimes concave, the smaller two 1.5-2.5 mm long; wings suborbicular to suborbicular-obovate, hooded, broadly rounded apically, rounded or rounded-cuneate basally, rarely ciliate on the margin, occasionally sparsely pubescent within, 3.5-5 mm long, 3-4.2 mm wide; keel orbicular, usually plicate laterally, emarginate apically, 4-7 mm long, 5-7.8 mm wide, rarely ciliate on the lower part of the margin, sparsely pubescent within or glabrous; upper petals yellow, spatulate, pubescent within, sparsely pubescent or glabrous on the outside, 3.8-5.4 mm long; staminal sheath pilose apically, the free part of the filaments 0.7-1.4 mm long; ovary ellipsoidal, 1.1-1.8 mm long, 0.9-1.1 mm wide, usually glabrous, rarely pubescent, the style usually geniculate, 2.3-3 mm long, the stigma 2-lobed, the outer acute, the inner tubercled. *Drupe* ovoid, obtuse or emarginate, conspicuously rugose-reticulate, glabrous, 5-8 mm long, 3.5-4.5 mm wide.

Mexico to Panama at higher elevations.

CHIRIQUI: llanos on slopes of Volcán de Chiriquí Viejo & along Río Chiriquí Viejo, alt 1200 m, *Allen 984* (MO); trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt 1500-2000 m, *Allen 1576* (MO); vic of Boquete, lumber rd into hills E of Río Caldera, *Allen 4662* (MO); Bajo Mono-Robalo Trail, W slopes of Cerro Horqueta, alt 5000-7000 ft, *Allen 4791* (MO); Cerro Horqueta, alt ca 1500 m, *Duke 13653* (MO); Fred Collins Finca, edge of coffee plantation, alt 6000 ft, *Ebinger 661* (MO); vic of Boquete, from Boquete to 3 miles N, second growth, cultivated areas, roadsides, alt 3300-4200 ft, *Lewis et al. 412* (MO), *413* (MO); vic of Cerro Punta, cloud forest & disturbed edge, alt 6800 ft, *Ridgway & Solís 2408* (F, MO); Cerro Horqueta, cloud forest, alt 6500 ft, *von Hagen & von Hagen 2074* (MO); betw Concepción & El Volcán, *White 311* (MO); vic of Bajo Mona & Quebrada Chiquero, alt 1500 m, *Woodson & Schery 540* (MO). COCLE: betw Cerro Pilón & El Valle de Antón, cloud forest, alt 700-900 m, *Duke & Dwyer 13900* (GH, MO); El Valle de Antón at foot of Cerro Pilón, cloud forest, alt ca 2000 ft, *Dwyer & Correa 7959* (GH, MO); summit of Cerro Pilón, above El Valle de Antón, rain forest, alt ca 2700 ft, *Dwyer et al. 4500* (MO); mountains beyond La Pintada, alt 400-600 m, *Hunter & Allen 545* (MO); mountains N of El Valle de Antón, cloud forest, alt 2500-3000 ft, *Lewis et al. 1735* (COL, MO, UC, US); El Valle de Antón, edge of cloud forest & roadside, alt 1000-2000 ft, *Lewis et al. 2539* (DUKE,

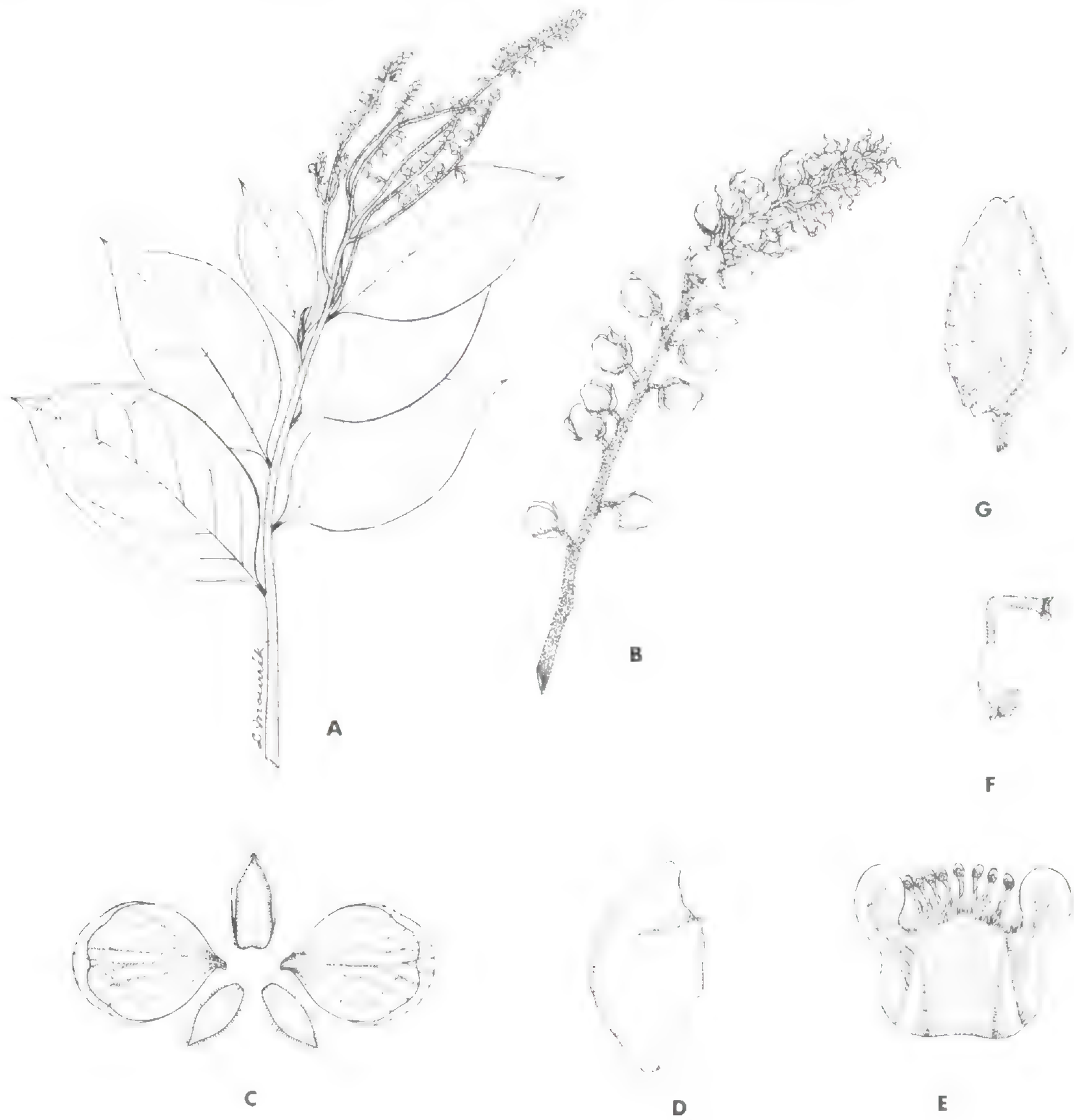

Fig. 2. *Monnina sylvatica* Schlecht. & Cham.: A, habit (× 1/3); B, inflorescence (× 1); C, sepals (× 3½); D, keel (× 3½); E, stamens and upper petals (× 3½); F, pistil (× 3½); G, fruit (× 3½). After *Lewis et al.* 2539 (MO).

K, MO, NY); Cerro Pilón, alt 2000 ft, *Porter et al.* 4603 (MO). LOS SANTOS: Cerro Pilón, rain forest, alt 2700 ft, *Duyer & Lallathin* 8612 (MO).

2. **Monnina xalapensis** H.B.K., Nov. Gen. Sp. Pl. **5:** 414, 1823.

M. latisepala Blake, N. Amer. Fl. **25:** 376, 1924.

Herbs, shrubs or even small trees to 6 m high; branches striate, short-strigose or becoming ± glabrescent. *Leaves* oblanceolate, elliptic, or obovate-elliptic, acute to acuminate, sometimes cuspidate or falcate apically, acute to acuminate basally, 3-10 cm long, 1-3.5 cm wide, membranaceous to chartaceous, rather sparsely pubescent on both sides, usually more densely so along the costa and veins beneath, sometimes glabrescent, the costa prominulous beneath with 5-7 pairs of lateral veins; petioles 3-12 mm long, pubescent. *Racemes* not at all comose, to

3.5 cm long and 1.5 cm wide, terminal or axillary; peduncles to 1.5 cm long, the axis 10 cm or less, conspicuously pubescent; bracts triangular-ovate, acute or obtuse, ciliate and pubescent, deciduous, 1.4-2.2 mm long. *Flowers* purple or blue; pedicels 1-2.4 mm long, pubescent; outer sepals free, triangular- or oblong- to suborbicular-ovate, acute to obtuse, sometimes mucronate at the obtuse apex, margin ciliate, short-pubescent or glabrescent outside, 2.5-3.2 mm long, usually all 3 ca equal, sometimes the upper sepal slightly longer and concave, usually the lower 2 with a small lateral lobe; wings suborbicular, hooded, broadly rounded apically, cuneate basally, usually ciliate on the margin, sparsely pubescent within, 5-6.2 mm long, 4.5-6 mm wide; keel orbicular, plicate laterally, emarginate apically, 5.5-6.5 mm long, 5-7.8 mm wide, rarely ciliate on the lower part of the margin, glabrous within; upper petals yellow, spatulate, pubescent within, sparsely pubescent or glabrous on the outside, 3.4-4.8 mm long; staminal sheath pilose apically, the free part of the filaments 0.8-1.2 mm long; ovary ellipsoidal to ovoid, 1.3-2 mm long, 0.8-1 mm wide, pubescent or glabrous, the style geniculate, 2.5-3.5 mm long, the stigma 2-lobed, the outer acute, the inner tubercled. *Drupe* ellipsoid-ovoid, obtuse, rugose-reticulate, glabrous, 6-7.5 mm long, 3.5-4 mm wide.

Mexico to Panama at higher elevations.

CHIRIQUI: trail from Bambito to Cerro Punta, 1400-2300 m, *Allen 318* (MO) (as *M. pittieri* Chodat); summit & SW face of Cerro Copete, alt 9000 ft, *Allen 4899* (MO); Volcán de Chiriquí, alt 7000 ft, *Davidson 889* (A, MO); Alto de Cuesta, *Pittier 3119* (holotype of *M. latisepala* US; isotype NY); valley of upper Río Chiriquí Viejo, vic of Monte Lirio, alt 1300-1900 m, *Seibert 306* (MO); Río Chiriquí Viejo valley, *White 49* (MO); Chiriquí, valley of upper Río Chiriquí Viejo, in open sunlight, *White & White 26* (A, MO, NY) (as *M. pittieri* Chodat?); Finca Lérida to Peña Blanca, alt 1750-2000 m, *Woodson & Schery 304* (MO); Casita Alta to Cerro Copete, alt 2300-3300 m, *Woodson & Schery 338* (GH, MO); Potrero Muleto to summit, Volcán de Chiriquí, 3500-4000 m, *Woodson & Schery 441* (GH, MO); vic of Casita Alta, Volcán de Chiriquí, alt 1500-2000 m, *Woodson et al. 802* (A, MO). PROVINCE UNKNOWN: Sierra Madre, *Seemann s.n.* (GH).

We suspect that *M. xalapensis* and *M. sylvatica* hybridize; one collection from Cerro Horqueta at 5000-5800 ft [*Dwyer et al. 435* (MO, UC, US)] is intermediate between these species and is considered a putative hybrid.

4. MOUTABEA

Moutabea Aublet, Hist. Pl. Gui. Fr. 679, *t. 247*, 1775.

Erect or scandent *shrubs* or small trees. *Leaves* alternate, petiolate, the blades thick and coriaceous, usually glabrous. *Racemes* short, axillary. *Flowers* white or yellow; calyx adnate with the corolla into a tube, the sepals 5, ± equal, the petals 5, subequal with the lower slightly boat-shaped; stamens 8, joined into 2 groups of 4 on the margin of an oblique sheath which is adnate to the corolla-tube, the anthers sessile; ovary 4- or rarely 2- to 5-locular, surrounded by a disc, the ovules 1, pendulous, the style filiform, slightly dilated apically. *Berry* (drupaceous?) globose, indehiscent, 2-5-seeded, edible; seeds shining in the fleshy pericarp, without aril or endosperm.

Perhaps 10 species of tropical South America and Panama; only one in Panama, a first record for the genus in North America.

1. **Moutabea** aff. **longifolia** Poeppig & Endl., Nov. Gen. Sp. Pl. **2:** 62, *t. 186,* 1838.

Shrubs 2.2 m tall, the branches with dark, straight hairs. *Leaves* with short, thick petioles 1 cm long; blades oblong to obovate, glabrous, prominently reticulate-veined above and below, ca 17 cm long and ca 7 cm at widest point 12 cm from the petioles. *Racemes* terminal and axillary, several per axis, the peduncles to 2.5 cm long, sparsely puberulent with numerous puberulent ovate bracts 2 mm long. *Flowers* white (drying almost black), tubular; tube 1 cm long; sepals 6-8 mm long, pubescent within; petals 8-10 mm long, linear-spatulate, pubescent within; 8 sessile anthers grouped 4 on each margin of the sheath, the margin 2-3 mm long. *Fruit* unknown.

COCLE: Bismark above Penonomé, *Williams* 565 (US).

Allied to and perhaps conspecific with *M. longifolia* of South America which, however, has more lanceolate leaves. A second specimen collected by Williams (966) in Darien (Cana & vic, US) may also prove to be a species of *Moutabea.* The material is sterile but the leaves closely approximate those of the original plate of *M. longifolia.*

INDEX OF LATIN NAMES

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

Elsota 21
  chrysotrica 23, 24†
  tenuifolia 23
Monnina **24**
  crispata 25
  latisepala 26, 27†
  pittieri 27†
  sylvatica **25,** 27†
  xalapensis **26,** 27†
Moutabea 9†, **27,** 28†
  aff. longifolia **28**
  longifolia 28†
Polygala 9†, **9**
  angustifolia 11
  aparinoides **19**
  asperuloides 19†, **19**
  brizoides **11**
  costaricensis 12†
  diversifolia 22
  durandii 12†
  fendleri var. heterothrix **12**
  hygrophila **15**
  jefensis **21**
  leptocaulis **13**
  longicaulis **16,** 18†
  monticola 12†
  panamensis **12**
  paniculata 13†, **14**
  timoutou **18**
  variabilis **18**
  wurdackiana **20,** 21†
Securidaca **21**
  coriacea 24†
  diversifolia **22,** 23†
  pubescens 23†
  —*β* ovata 23†
  tenuifolia **23,** 24†
  tomentosa 23†
  volubilis 23†

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 161. MENYANTHACEAE[1]

BY THOMAS S. ELIAS[2]
St. Louis University, St. Louis, Missouri

Herbs, aquatic or semiaquatic. *Leaves* alternate, entire, simple or trifoliolate, often orbicular and peltate, petiole sheathing at the base, exstipulate. *Inflorescences* racemose, solitary, paired, or fasciculate, or in many-flowered cymes, panicles, or involucrate heads. *Flowers* bisexual, regular; calyx 5-merous, free or fused basally; corolla 5-merous, fused basally to form a short tube, the lobes valvate or induplicate-valvate, the margins and/or interior often fimbriate or barbate; stamens 5, alternate with the petals and inserted near the base of the corolla tube, the anthers 2-locular, sagittate, versatile; hypogynous nectaries usually present; pistil 1, the ovary superior, 1-locular, with 2 parietal placentas, ovules ∞, the style simple, the stigma bifid. *Fruit* a capsule, 2- or 4-valved, rarely fleshy and indehiscent; seeds few to numerous, sometimes winged, endosperm copious, embryo small.—$x = 9, 17$.

A small family of five genera and ca 30-35 species occurring in temperate and tropical regions of both hemispheres. The genera have been included by earlier workers (Bentham & Hooker, Gen. Pl. **2:** 819, 1876; Gilg in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 62, 1876) as a tribe or subfamily of the *Gentianaceae*. Later workers (Hutchinson, Fam. Fl. Pl. **1:** 451, ed. 2, 1959; Cronquist, Evol. & Class. Fl. Pl. 288-289, 1968) have maintained them as a distinct family, separated from the *Gentianaceae* by the alternate leaves and the valvate or induplicate-valvate aestivation. Only the genus *Nymphoides* is found in Panama.

1. NYMPHOIDES

Nymphoides Séguier, Pl. Veron. **3:** 121, 1754.

Limnanthemum S. G. Gmel., Novi Comment. Acad. Sci. Imp. Petrop. **14**(1): 525, 1770.

Herbs, aquatic, perennial; stems petiole-like. *Leaves* simple, usually broadly ovate or orbicular, peltate, cordate at the base, floating. *Flowers* white or yellow; calyx basally fused; corolla broadly campanulate or almost rotate, the lobes fimbriate; stamens included, the anthers ovate to linear; ovary ellipsoid, the style short,

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[1]Assisted by National Science Foundation Grant No. GB-5674.

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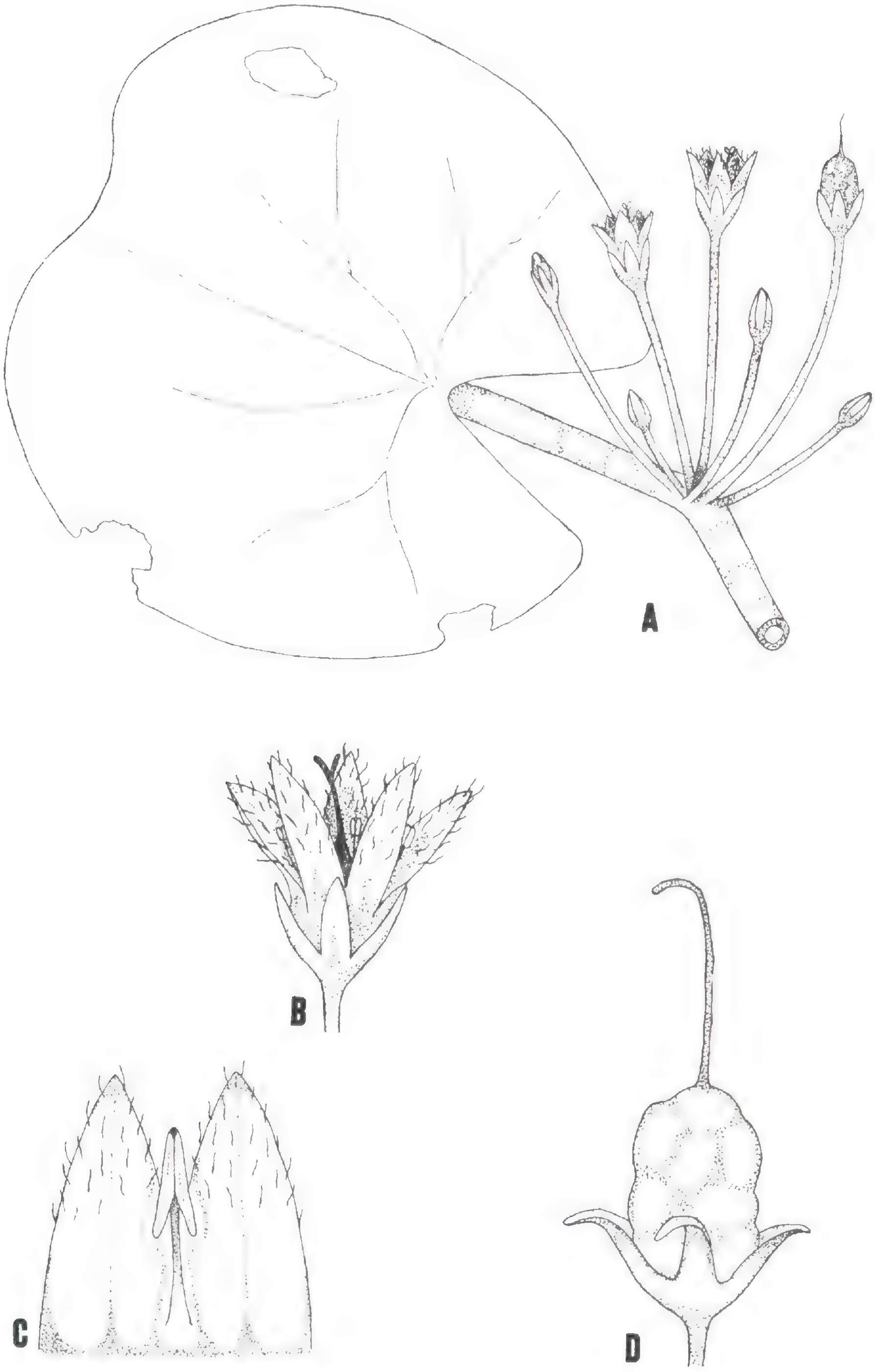

Fig. 1. *Nymphoides humboldtianum* (H.B.K.) O. Kuntze: A, habit (× ½); B, flower (× 2½); C, two corolla lobes and a stamen (× 5); D, fruit with marcescent calyx and style (× 5). After *Croat 8215* (MO).

the stigmas usually broad. *Capsules* indehiscent or eventually rupturing irregularly, firm-walled; seeds many, unwinged, the seed coat hard.—$x = 9$.

A small genus of ca 20 species chiefly of tropical and subtropical areas in the New and Old Worlds. Only one species is known from Panama, the common *N. humboldtianum*.

Nymphoides humboldtianum (H.B.K.) O. Kuntze, Rev. Gen. Pl. **2:** 429, 1891. (as *Nymphodes*).—Fig. 1.

Villarsia humboldtianum H.B.K., Nov. Gen. Sp. Pl. **3:** 187, 1819.
Limnanthemum humboldtianum (H.B.K.) Griseb., Gen. Sp. Gent. 347, 1839.

Herbs aquatic, from submerged rhizomes; stems 8-150 cm long, to 6 mm in diam, ascending, green, glandular (?) dotted near the apex, succulent, weak, vertically septate with several continuous air spaces, the stems with a single terminal leaf or usually branching near the apex to give rise to an inflorescence and additional leaves. *Leaves* orbicular to subovate, cordate at the base, often deeply so, obtuse at the apex, often becoming emarginate on the larger leaves, 2-18 cm in diam, succulent, green above, dark reddish-violet beneath, coriaceous. *Inflorescences* of many fascicled flowers, appearing umbellate, axillary. *Flowers* white, 1-8 cm long, pedicellate, the pedicels (mature) 3-7 cm long, succulent, glandular (?) dotted, erect to suberect; calyx-lobes lanceolate, acute to short apiculate at the apex, the margins scarious, 4.5-8 mm long; corolla 1-1.8 cm long, the lobes ovate to ovate-oblong, acute at the apex, very membranous, ± transparent when dried, 8-12 mm long, conspicuously fimbriate, the hairs 1-3 mm long, the lobes fused near the base; stamens introrse, 5-7 mm long, the filaments ca 3-5 mm long, ± flattened, the anthers 2 mm long, sagittate and spreading at the base; pistil 9-12 mm long, the ovary ellipsoid, sessile, 3-5 mm long, the style cylindrical, the stigma lobes to 1 mm long, flattened. *Capsules* indehiscent and eventually rupturing irreguarly, ellipsoid, 4-6 mm long, ca 10-18-seeded the persistent style rostrate; seeds orbicular, slightly flattened dorsiventrally, 1-1.2 mm long, shiny.

CANAL ZONE: Barro Colorado I, shore line, quiet water, *Croat 8215* (MO); Río Chagres, *Fairchild 2045* (MO); Madden Lake, *Woodson & Schery 958* (MO). COCLE: El Valle de Antón & vic, in bogs, *Seibert 440* (MO); betw Las Margaritas & El Valle de Antón, in bog, *Woodson et al. 1753* (MO). PANAMA: along rd betw Panama & Chepo, in pools in savannas, *Dodge et al. 16711* (MO); Sabanas, nr Chepo, in shallow pond, *Hunter & Allen 66* (MO), *Hunter & Steyermark s.n.* (MO); wet savanna E of Pacora, in lake, depth 1 m, *Woodson et al. 752* (MO).

A common aquatic herb in the West Indies and Central and South America, *N. humboldtianum* appears to be restricted to quiet and non-running waters. When growing in shallow bogs or marshes, the stems are considerably shortened. The length of the stem is apparently determined by the depth of the water in which it is growing. In marsh habitats in Panama the stems are ca 8-15 cm long *(Seibert 440, Woodson et al. 1753)*, while those growing in lakes have been observed to be as long as 1.5 m *(Croat 8215)*. In addition to shorter stems, the marsh or bog plants of this species have smaller leaves than those plants which

are found in lakes. The small-leaved populations were given varietal status (var. *parvifolium*) by Grisebach (Gen. Sp. Gent. 347, 1839).

Ornduff, in a treatment of the Meso-American and West Indian species of *Nymphoides*, suggests that *N. humboldtiana* is conspecific with the Old-World *N. indica* (L.) O. Kuntze. He makes his case very strongly, but I prefer to hold to the later name until the taxonomy of the *N. indica* complex is completely worked out.

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

Gentianaceae 29†
Limnanthemum 29
  humboldtianum 31
Nymphoides 29†, **29**
  humboldtianum 31†, **31**
  —var. parvifolium 32†
  indica 32†
Villarsia humboldtianum 31

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 167. BORAGINACEAE[1]

BY JOAN W. NOWICKE
Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Herbs, shrubs or trees, rarely lianas, frequently scabrous, the hairs simple, uniseriate, or stellate, often with a hardened base, or sometimes glabrous. *Leaves* alternate or sometimes opposite, simple, generally petiolate, the blade pinnately-nerved, entire or rarely dentate. *Inflorescences* cymes, generally helicoid or scorpioid, paniculate and open, spike-like, or glomerate, or rarely the flowers solitary, the bracts seemingly absent. *Flowers* perfect or functionally unisexual, actimorphic or rarely zygomorphic; bracteoles generally absent; sepals 5, rarely 4, free or connate basally, sometimes irregular; petals 5, united, salverform, funnelform, or campanulate, the lobes distinct or obscure, the tube sometimes with folds or appendages in the throat; stamens 5, functional or not, epipetalous, alternate with the corolla lobes, the filaments simple or with dorsal appendages, glabrous or fimbriolate basally, the anthers linear, introrse, dehiscing longitudinally; gynoecium syncarpous, 2-carpellate, ovary superior, bilocular and becoming falsely 4-locular, placentation axile, ovules 4, or fewer by abortion, anatropous, style one, gynobasic or terminal, simple, cleft, or twice cleft, stigmas 1, 2, or 4. *Fruit* 4 nutlets, a 1-4-seeded nut, or a drupe; seeds generally without endosperm. $x = 4, 10, 13$.

A widely-distributed family of about 100 genera and 2000 species. Seven genera are found in Panama.

The *Boraginaceae* are of little economic importance; a few are cultivated as ornamentals, and some species of *Cordia,* whose wood varies in color and weight, are utilized as a source of lumber.

Useful references:

Johnston, I. M. Studies in the *Boraginaceae,* XV. Notes on some Mexican and Central American species of *Cordia.* Jour. Arnold Arb. **21:** 336-355, 1940.

———. Studies in the *Boraginaceae,* XVII. A. *Cordia* section *Varronia* in Mexico and Central America. loc. cit. **30:** 85-104, 1949a.

———. Studies in the *Boraginaceae,* XVIII. *Boraginaceae* of the southern West Indies. loc. cit. **30:** 111-138, 1949b.

———. Botany of San José Island. Sargentia **7:** 1-306, 1949c.

KEY TO GENERA

a. Herbs.
   b. Nutlets with hooked spines; style gynobasic.

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[1] Assisted by National Science Foundation Grant No. GB-5674.

c. Fruit distinctly 4-lobed, the nutlets attached at the apices; veins tending to form a network in the leaves ..... 1. *Cynoglossum*

cc. Fruit pyramidal, the nutlets attached medially; veins not forming a network in the leaves ..... 2. *Hackelia*

bb. Nutlets strigose or glabrous but without hooked spines; style terminal. 3. *Heliotropium*

aa. Shrubs, trees, or sometimes vines.

d. Styles and stigmas simple ..... 4. *Tournefortia*

dd. Styles once- or twice-divided, the stigmas 2 or 4.

e. Stigmas 2, capitate or peltate.

f. Calyx closed in bud; leaves entire ..... 5. *Bourreria*

ff. Calyx open in bud; leaves serrate ..... 6. *Ehretia*

ee. Stigmas 4, slender or clavate ..... 7. *Cordia*

1. CYNOGLOSSUM

Cynoglossum L., Sp. Pl. 134, 1753.

Herbs, mostly perennial, sometimes annual or biennial, slender to very robust, glabrous to coarsely pubescent. *Leaves* alternate, simple, pinnately-nerved, entire, the basal ones long-petiolate. *Inflorescences* racemes or irregular panicles, scorpioid, the bracts mostly not apparent. *Flowers* perfect, actinomorphic; calyx of 5 sepals, ± connate basally, enlarging somewhat in fruit; corolla salverform, funnelform, or ± campanulate, blue, violet, or reddish, 5-lobed, the lobes ± spreading, 5 faucal appendages generally well-developed; stamens 5, included or barely exserted at the corolla throat, subsessile or the filaments very short, the anthers oblong; ovary 4-lobed, distinctly so, the gynobase disc-like, the style gynobasic, the stigma 1 and ± capitate. *Fruits* 4 nutlets, spreading at maturity, adnate apically to the gynobase, the scar not extending below the middle on the ventral side, the surface covered with stout, glochidiate spines.

A cosmopolitan genus of about 80 species.

1. **Cynoglossum amabile** Stapf & Drum., Kew Bull. **1906:** 202, 1906.—Fig. 1B.

Herbs, weedy, to ca 0.5 m, densely strigose. *Leaves* lanceolate or ± lanceolate-elliptic, acute, sometimes bluntly so, entire, the bases obtuse to attenuate, to 9 cm long and 2 cm wide, densely strigose, the veination somewhat netlike; stem leaves ± sessile, basal leaves with petioles to ca 5 cm long. *Inflorescences* racemes, scorpioid, to ca 15 cm long, borne in irregular panicles, axillary or terminal. *Flowers* ± sessile to pedicels ca 3 mm long in fruit; sepals connate basally, ovate-elliptic, ca 1.8-2.8 mm long, strigose, the margins ciliate, persistent in fruit; corolla campanulate, blue, with 5 spreading ovate-rounded lobes, each ca 2-2.5 mm long and 2.5 mm wide, the tube closed at the throat by 5(-10) appendages with fimbriolate margins; stamens ± sessile, the anthers ca 1 mm long; style stout, ca 1.5-2 mm long, the stigma capitate. *Nutlets* ca 3-3.5 mm long.

Native to China, but widely introduced in Central America and also reported from northeastern North America.

CHIRIQUI: vic of Boquete, Finca Collins, *Blum & Dwyer 2580* (MO), *Stern et al. 1962* (MO); NW of Boquete, Cerro Horqueta, *Dwyer et al. 443* (MO).

2. HACKELIA

Hackelia Opiz in Bercht., Fl. Boehm. **2**(2): 146, 1838.

Herbs, mostly perennial, rarely biennial or annual, ± glabrous to pubescent. *Leaves* alternate, mostly narrow, entire, the basal ones sometimes long petiolate. *Inflorescences* raceme-like, scorpioid, tending to elongate in age, bracts absent or leaf-like on the lower flowers. *Flowers* perfect, mostly actinomorphic or weakly zygomorphic; calyx of 5 sepals, ± free or connate basally; corolla salverform to funnelform, white or blue, often with a yellow center, 5-lobed, the lobes equal or ± unequal, 5 faucal appendages variously developed; stamens 5, included, the filaments short, the anthers linear; ovary 4-lobed, distinctly so, gynobase disc-like and somewhat lobed, the style simple and gynobasic, the stigma capitate. *Fruit* 4 nutlets, medially adnate to the gynobase, the scar conspicuous, the dorsal side with glochidiate spines, the spines larger along the margins, sometimes 2 of the nutlets with short spines and 2 with longer spines.

A genus of about 30 species, widely distributed, but centered in western North America. One species is found in Panama.

Useful reference:

Johnston, I. M. Studies in the *Boraginaceae.* I. Restoration of the genus *Hackelia.* Contr. Gray Herb. **68:** 43-48, 1923.

1. **Hackelia mexicana** (Schlecht. & Cham.) I. M. Johnston, Contr. Gray Herb. **68:** 46, 1923.—Fig. 1A.

Cynoglossum mexicanum Schlecht. & Cham., Linnaea **5:** 114, 1830.
Lappula costaricensis Brand, Repert. Spec. Nov. **18:** 310, 1922.
Hackelia costaricensis (Brand) I. M. Johnston, Contr. Gray Herb. **68:** 46, 1923.

Herbs, somewhat suffrutescent basally, to 1.5 m, the branches pubescent, the hairs white. *Leaves* elliptic to obovate, acute or ± acuminate, entire, the bases obtuse to long-attenuate, the basal leaves exaggeratedly so, to 12 cm long and 5 cm wide, pubescent on both surfaces, more so on the veins beneath; subsessile to petioles 18 cm long for basal leaves. *Inflorescences* racemes, scorpioid, elongating in fruit. *Flowers* with pedicels ca 1-5 mm long; bracteole single, leaf-like, size variable; calyx of 5 sepals, weakly connate basally, the lobes subulate or deltoid, ca 2-3 mm long, pubescent; corolla funnelform, weakly zygomorphic, blue, the tube ca 1.5 mm long, the lobes oblong, ± unequal, ca 1.6-2.2 mm long and 1.4-2 mm wide, with 5 faucal appendages opposite the lobes; stamens subsessile, the anthers ca 0.5 mm long; ovary 4-lobed, distinctly so, disc present, the style gynobasic, the stigma capitate. *Fruit* 4 nutlets, ± pyramidal, connate apically, ca 2 mm high, covered with glochidiate spines, the spines sometimes of 2 distinct lengths, 2 nutlets with long spines and 2 nutlets with shorter spines.

Mexico and Central America.

CHIRIQUI: vic of Cerro Punta, *Blum et al. 2422* (MO), *Ridgway & Solis 2394* (MO); Potrero Muleto, *Davidson 1018* (MO); vic of Casita Alta, *Woodson et al. 890* (MO).

Fig. 1. *Hackelia mexicana* (Schlecht. & Cham.) I. M. Johnston: A, fruiting branch (× 5/7). After *Ridgway & Solis 2394* (MO). *Cynoglossum amabile* Stapf & Drum.: B, fruiting branch (× 5/7). After *Stern et al. 1962* (MO.)

3. HELIOTROPIUM

Heliotropium L., Sp. Pl. 130, 1753.

Herbs, sometimes suffrutescent, rarely shrubs, ± glabrous to roughly pubescent. *Leaves* alternate, sometimes ± fasciculate, pinnately-veined, small to large. *Inflorescences* spikes or racemes, scorpioid, solitary, paired, or ternate, or the flowers solitary, bracts present or absent. *Flowers* perfect, ± actinomorphic or weakly zygomorphic, pedicellate or subsessile; calyx of 5 sepals, ± connate basally, persistent or deciduous, the lobes linear or lanceolate; corolla mostly salverform to funnelform, white, yellow or blue, the limb 5-lobed, the lobes ± spreading, the throat without appendages; stamens 5, included, borne on the corolla throat, the filaments short or absent, the anthers linear; ovary 4-loculed, lobed or unlobed, a glandular ring at the base, the style apical, the stigmas sessile or not, peltate or conic. *Fruit* lobed or unlobed, dry, separating into 2-4 nutlets at maturity; nutlets 1-2-seeded.

About 200 species in the warmer regions of both hemispheres. Three species are known from Panama, but at least one other, *H. lagoense* (Warm.) Gürke, which has very distinctive long-pedicellate flowers, has also been reported as occurring there (Johnston, Jour. Arnold Arb. **30:** 134, 1949). However, I have not seen material of this species from Panama and therefore have not included it.

a. Robust herbs; at least some leaves > 4 cm wide; inflorescences > 10 cm long ..... 1. *H. indicum*

aa. Decumbent herbs; leaves > 1.5 cm wide; inflorescences < 9 cm long.

b. Plants glabrous; leaves somewhat succulent, usually glaucous.... 2. *H. curassavicum*

bb. Plants pubescent, the hairs white; leaves not succulent nor glaucous. 3. *H. procumbens*

1. **Heliotropium indicum** L., Sp. Pl. 130, 1753.

Heliophytum indicum (L.) DC., Prodr. **9**: 556, 1845.

Herbs, annual, coarse and weedy, to 1.5 m, the stems with short and longer hairs. *Leaves* alternate, ovate, or sometimes ± deltoid, acute, finely to coarsely undulate, the bases obtuse to rounded and long-attenuate, to 11 cm long and 6.5 cm wide, sparsely pubescent on both surfaces, the veins prominent beneath; petioles ± winged or indistinct, to 8 cm long. *Inflorescences* spicate, scorpioid, to ca 28 cm long, mostly terminal, the bracts absent. *Flowers* sessile; calyx of 5 free sepals, subulate, ca 1.5-2 mm long; corolla salverform, blue, violet, or rarely white, the tube ca 3-4 mm long, each lobe ca 1 mm long; stamens ± sessile, the anthers ca 0.6-0.8 mm long; ovary weakly 4-lobed, the style somewhat stout, the stigma conical. *Fruit* deeply 4-lobed, the lobes horizontally divergent, separating into 4 nutlets at maturity, the nutlets angulate, glabrous to sparsely strigose, 2-3 mm long.

A roadside weed, widely distributed in Panama and in the American Tropics.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Old Bank I, *von Wedel 1968* (MO). CANAL ZONE: s. loc., *Eppelsheimer s.n.* (F). COCLE: 12 mi NE of Penonomé, *Lewis et al. 1524* (MO). DARIEN: vic of El Real, Río Tuira, *Stern et al. 452* (MO). LOS SANTOS: Río Tonosí, vic of Tonosí, *Lewis et al. 1558* (MO). PANAMA: roadside betw Chepo & wharf, *Dodge s.n.* (F); San Miguel I, *Duke 10937* (MO); Taboga I, *MacBride 2792* (F, MO). VERAGUAS: 2 mi S of Canazas, *Tyson 3725* (MO).

A medicinal tea is made by boiling the leaves.

2. **Heliotropium curassavicum** L., Sp. Pl. 130, 1753.

Herbs, prostrate, the stems 0.5 m long or longer, glabrous, succulent, sometimes glaucous on the younger parts. *Leaves* alternate or somewhat fasciculate, oblanceolate, lanceolate, or spatulate, obtuse, entire, the bases attenuate, to 4 cm long and 1 cm wide, glabrous, succulent, somewhat glaucous; petioles indistinct. *Inflorescences* ± spikes, unilateral, mostly terminal, ca 2-5 cm long, the bracts absent. *Flowers* sessile, ± actinomorphic; calyx of 5 sepals, slightly connate basally, elongate-deltoid, ca 1.2-1.5 mm long; corolla salverform, white, the tube somewhat saccate, ca 1.2 mm long, each lobe ca 0.8 mm long; stamens 5, ± sessile, the anthers ca 0.6-0.7 mm long; ovary 4-lobed, the disk obscure, the style absent, the stigma conical, annular-pubescent at the widened base. *Fruit* 4-lobed, separating into 4 nutlets at maturity, the nutlets glabrous, wedge-shaped, ca 1.6-1.7 mm long.

Widely distributed in the warmer regions of America, particularly along coasts and inland on saline soils.

LOS SANTOS: Monagre Beach, *Dwyer 4177* (MO), *Tyson et al. 3023* (MO).

3. **Heliotropium procumbens** Mill., Gard. Dict. ed 8, no. 10, 1768.—Fig. 2.

H. inundatum Sw., Prodr. 40, 1788; non L., Sp. Pl. 130, 1753.

Herbs, prostrate, somewhat wiry, the stems 15-20 cm long, pubescent, the hairs white. *Leaves* alternate, ± elliptic to ovate, bluntly acute, entire, the bases obtuse, to 1.5 cm long and 0.8 cm wide, pubescent on both surfaces, the hairs with enlarged bases; petioles ca 3-5 mm long. *Inflorescences* spike-like, unilateral, to 7 cm long, the bracts absent. *Flowers* ± sessile; calyx of 5 sepals, slightly connate basally, the lobes lanceolate, subequal, ca 1 mm long, pubescent; corolla weakly salverform, white, the tube ca 0.8 mm long, sparsely pubescent, the lobes ± unequal, erect, and ca 0.2-0.4 mm long; stamens 5, ± sessile, the anthers ca 0.2 mm long; ovary 4-lobed, the style absent, the stigma conic. *Fruit* 4-lobed, separating into 4 nutlets at maturity, the nutlets wedge-shaped, strigose, ca 0.4-0.5 mm long.

Widely distributed in the warmer parts of America.

LOS SANTOS: Río Tonosí, vic of Tonosí, *Lewis et al. 1575* (MO).

4. TOURNEFORTIA

Tournefortia L., Sp. Pl. 140, 1753.

Shrubs, sometimes decumbent, vines, or small trees, glabrous to densely pubescent. *Leaves* alternate, sometimes opposite, simple, pinnately-nerved; sessile or petiolate. *Inflorescences* cymose, scorpioid, sometimes borne in irregular panicles, the bracts seemingly absent. *Flowers* perfect, ± actinomorphic, sessile or shortly pedicellate; calyx of 5 sepals, free or weakly connate basally, lanceolate to ovate, ± glabrous to densely strigose; corolla white, yellow, or ± green, salverform or funnelform, glabrous or strigose, the tube cylindrical, the limb usually 5-lobed and spreading, the lobes frequently keeled; stamens (4-)5, rarely more, borne on the corolla throat, included, the filaments very short, the anthers elongate, free,

Fig. 2. *Heliotropium procumbens* Mill.: A, habit (ca × 5/8); B, flower (ca × 15). After *Lewis et al. 1575* (MO).

or ± connate apically; ovary 2-carpellate, each carpel with two ovules, disc ± distinct, sometimes cup-shaped, style long and slender or ± absent, the stigma peltate or conic. *Fruit* fleshy, ± globose and unlobed to distinctly 4-lobed, separating into 2-4 nutlets at maturity.

A large genus of about 120 poorly-defined species in the warmer regions of the world, but centering in the neotropics. Eight species are found in Panama.

a. Fruits distinctly 2-4-lobed; anthers connate apically.
  b. Leaves with dense, curled pubescence; corolla tube < 2.5 mm long; style ca 1 mm long ..... 1. *T. volubilis*
  bb. Leaves pubescent, but the hairs not dense nor curled; corolla tube ca > 3 mm long; style elongate and delicate, ca 2-3 mm long ..... 2. *T. maculata*

aa. Fruits pyramidal or globose, not 2-4-lobed; anthers free apically.
  c. Flowers with a long corolla tube, 10-12 mm, and short sepals, ca < 1.5 mm long ..... 3. *T. angustiflora*
  cc. Flowers without the above combination of a long corolla tube and short sepals.
    d. Plants essentially glabrous on the stems.
      e. Branches of the inflorescence elongate; stigma on a short style; leaves membranaceous ..... 4. *T. glabra*
      ee. Branches of the inflorescence short and tightly scorpioid; stigma ± sessile; leaves coriaceous ..... 5. *T. bicolor*
    dd. Plants conspicuously pubescent on stems, leaves, and sometimes fruits.
      f. Inflorescences densely-flowered, markedly scorpioid; sepals mostly 2-6 mm long.
        g. Stem hairs 4-6 mm long; leaves acuminate apically ..... 6. *T. cuspidata*
        gg. Stem hairs 1-2 mm long; leaves acute apically ..... 7. *T. hirsutissima*
      ff. Inflorescences once or twice dichotomously branched, the branches elongate; sepals very long, ca 8-10 mm ..... 8. *T. johnstonii*

1. **Tournefortia volubilis** L., Sp. Pl. 140, 1753.—Fig. 3.

Vines, woody, the stems with curled, appressed hairs. *Leaves* alternate, ± ovate, acute, entire, the bases obtuse or slightly rounded, ca 4-6 cm long and 1.5-2.5 cm wide, pubescent on both surfaces, the hairs curled and very dense beneath; petioles ca 0.5-1 cm long. *Inflorescences* cymose, arranged in open panicles, the branches 3-4 cm long. *Flowers* sessile to pedicels ca 1 mm long in fruit; calyx of 5 sepals, slightly connate basally, lanceolate, ca 1 mm long, pubescent; corolla white, pubescent, the tube ca 2 mm long; the limb 5-lobed, the lobes subulate and ca 1.5-1.8 mm long; stamens 5, ± sessile, the anthers ca 0.6-0.7 mm long, connate apically; ovary ovoid, the style about equal to the sepals, the stigma conical. *Fruit* distinctly (1-)2-4-lobed, ca 3-4(?) mm in diam.

Florida, Mexico, Central America, the West Indies, and South America.

LOS SANTOS: Monagre Beach, *Dwyer 4182* (MO).

An extremely variable species closely related to *T. maculata, Tournefortia volubilis* may be distinguished by its dense, curled pubescence, shorter corolla tube, and more delicate appearance of the inflorescence.

2. **Tournefortia maculata** Jacq., Enum. 14, 1760.—Fig. 4.

T. syringaefolia Vahl, Symb. **3**: 23, 1794.
T. peruviana Poir., Encyc. Suppl. **4**: 425, 1816.

Shrubs, decumbent, or small trees to 5 m, the younger parts pubescent. *Leaves* alternate, ± elliptic to ovate, entire, acute to acuminate, the bases obtuse or rarely

Fig. 3. *Tournefortia volubilis* L.: A, habit (ca × ¾); B, under surface of leaf (ca × 1.5). After *Dwyer 4182* (MO).

oblique, to 14 cm long and 5 cm wide, ± glabrous to moderately pubescent on both surfaces; petioles to ca 2 cm long. *Inflorescences* cymose, arranged in irregular panicles, the branches to 5 cm long. *Flowers* sessile or with pedicels to 2 mm long in fruit; calyx of 5 free sepals, deltoid or ovate-elliptic, ca 1.5-2 mm long,

Fig. 4. *Tournefortia maculata* Jacq.: A, fruiting branch (× 3/8); B, flowering branch (× 3/8). A, after *Tyson et al.* 4284 (MO); B, after *Davidson* 853 (MO).

sparsely scurfy to lightly strigose; corolla white to pale yellow-green, the tube ca 4-5 long, the lobes subulate, each < 1 mm long, ± scurfy; stamens 5, borne ca halfway up corolla tube, sessile, the anthers ca 1 mm long, connate apically; ovary ovoid, the style delicate, ca 2-3 mm long, the stigma conical. *Fruit* orange to yellow, distinctly (2-) 4-lobed, ca 4-5 mm wide, separating into (2-)4 nutlets at maturity.

Mexico, Central America, the West Indies, and northwestern South America.

CANAL ZONE: Barro Colorado I, *Bailey & Bailey* 237 (F); Ft San Lorenzo, *Maxon 7011* (F). CHIRIQUI: Boquete, *Davidson* 853 (MO). COCLE: betw Las Margaritas & El Valle, *Woodson et al. 1279* (MO). LOS SANTOS: Loma Prieta, *Duke 11879* (MO). PANAMA: Cerro Azul, Goofy Lake, *Dwyer 2412* (MO); San Jose I, *Erlanson 114* (GH), *501* (GH); rd from Chepo to El Llano, *Tyson & Smith 4119* (MO); Taboga I, *Woodson et al. 1471* (MO). VERAGUAS: Coiba I, *Dwyer* 2330 (MO); 5 mi E of Santiago, *Tyson et al. 4284* (MO).

3. **Tournefortia angustiflora** Ruiz & Pav., Fl. Peru. **2:** 25, *pl. 151,* 1799.

T. billbergiana Beurl., Kongl. Vetensk. Acad. Handl. Stock. 139, 1854.

Shrub to 3 m, or vine-like, sparsely pubescent. *Leaves* alternate, elliptic, lanceolate-elliptic, or rarely ovate-elliptic, entire, acute, the bases obtuse, to 15 cm long and 8 cm wide; petioles to ca 1.5 cm long. *Inflorescences* spikes, scorpioid, to 6 cm long. *Flowers* sessile; calyx of 5 sepals, slightly connate basally, broadly ovate, ca 1.2-1.5 mm long, ± glabrous to sparsely strigose; corolla white to yellow, glabrous to sparsely strigose, the tube ca 10-12 mm long, the lobes keeled, each ca 2 mm long; stamens 5, borne halfway up the corolla tube, ± sessile, the anthers ca 2 mm long; ovary ovoid, the style absent, the stigma closely appressed on the ovary. *Fruit* pyramidal, ca 4-5 mm in diam, the exocarp fleshy, separating into 4 nutlets at maturity.

From Honduras to Peru, common in Panama.

BOCAS DEL TORO: 10-15 mi from mouth of Río Changuinola, *Lewis et al. 876* (MO); Chiriquí Lagoon, Water Valley, *von Wedel 1600* (MO), *1785* (MO), *1802* (MO), *1832* (MO), Old Bank I, *von Wedel 2004* (MO); vic of Chiriquí Lagoon, Colon I, *von Wedel 2867* (MO), *2960* (MO). CANAL ZONE: W end Gatun Lake Dam, *Blum & Tyson 2000* (MO); Barro Colorado I, *Woodworth & Vestal 378* (A). COCLE: vic of El Valle de Antón, *Allen 2059* (MO). DARIEN: El Real, Quebrada Trapiche, *Duke & Bristan 315* (MO); Cocalito, *Duyer 4465* (MO). HERRERA: 10 mi S Ocú, *Tyson et al. 2863* (MO). PANAMA: nr Chepo, *Hunter & Allen 94* (MO). SAN BLAS: mouth of Río Ailigandí to 2.5 mi inland, *Lewis et al. 167* (MO).

The combination of long corolla tube and short sepals makes this species easily recognizable.

4. **Tournefortia glabra** L., Sp. Pl. 141, 1753.—Fig. 5.

Shrub, or small tree to 8m, ± glabrous. *Leaves* alternate, ± crowded, lanceolate-elliptic to ovate-elliptic, entire or very finely undulate, acute or acuminate, the bases obtuse, to 23 cm long and 10 cm wide, sparsely strigose on upper surface; petioles to ca 4 cm long. *Inflorescences* cymose, the branches elongate, ca 12(-30) cm long at maturity. *Flowers* sessile; calyx of 5 free sepals, subulate to lanceolate, sparsely strigose, ca 1.2-2(-3) mm long; corolla yellow to green, sparsely strigose, the tube ca 4-5 mm long, the lobes ca 1 mm long; stamens 5, borne ca halfway up the corolla tube, sessile, the anthers ca 1 mm long; ovary globose, the style ca 1 mm long, the stigma conical. *Fruit* globose, the exocarp ± fleshy, ca 4-5 mm in diameter, separating into 4 nutlets at maturity.

Mexico, Central America, and parts of the West Indies.

BOCAS DEL TORO: Almirante, Daytonia Farm, *Cooper 376* (MO); Chiriquí Lagoon, Water Valley, *von Wedel 1573* (MO), *1746* (MO). CHIRIQUI: Boquete, nr Chiquero, *Davidson 552* (MO); Cerro Horqueta, Cloud Forest Litter Study, *Duke et al. 13637* (MO); Boquete, Finca Collins, *Duver & Hayden 7644* (MO); Río Chiriquí Viejo Valley, nr Bambita, *White 46* (MO); Finca Lérida to Peña Blanca, *Woodson & Schery 285* (MO); vic of Casita Alta, Volcán de Chiriquí, *Woodson et al. 986* (MO). DARIEN: betw Quebrada Venado & Peje Swamp, *Bristan 1006* (MO); vic of Paya, Río Paya, *Stern et al. 396* (MO). PANAMA: Río Bayano nr PanAm Hwy, *Duke 3974* (MO), *3998* (MO).

Fig. 5. *Tournefortia glabra* L.: A, fruiting branch (× 3/8); B, flowering branch (× 3/8). After *Woodson & Schery* 285 (MO).

5. **Tournefortia bicolor** Sw., Prodr. 40, 1788.

T. laevigata Lam., Tab. Encyc. 1: 416, 1791.

Shrubs, scandent, or woody vines, the stems ± glabrous, or rarely sparsely pubescent, the hairs appressed. *Leaves* alternate, ± elliptic, acute or rarely acute-acuminate, entire, the bases obtuse, to 14 cm long and 7.5 cm wide, ± glabrous or rarely with appressed hairs, somewhat coriaceous, falcate, tending to dry brown-black; petioles ca 0.5-2 cm long. *Inflorescences* cymose, scorpioid, densely-flowered. *Flowers* sessile; calyx of 5 sepals, slightly connate basally, subulate, ca 1.5-2 mm long, glabrous; corolla white (yellow on drying), ± glabrous to sparsely strigose, the tube ca 4-5(-6) mm long, the lobes keeled, each ca 1.5-2(-2.5) mm long; stamens 5, borne ca ⅓ the way up the corolla tube, almost sessile, the anthers ca 1.5 mm long; ovary ovoid, the style absent, the stigma thick and conical. *Fruit* globose, white, ca 5-6 mm in diam, the exocarp fleshy, containing (1-)4 nutlets.

Widely distributed in the American Tropics, and well represented in Panama.

BOCAS DEL TORO: Water Valley, *von Wedel 986* (MO), *1838* (MO); vic of Chiriquí Lagoon, Old Bank I, *von Wedel 1952* (MO), *1992* (MO), Fish Creek Hills, *von Wedel 2427* (MO), Cocoa Cay, *von Wedel 2877* (MO). CANAL ZONE: Miraflores locks, Victoria Fill, *Allen 1713* (MO); Ft Clayton, *Dwyer* 3932 (MO); Barro Colorado I, *Shattuck s.n.* (MO), *807* (MO); nr Gorgas Memorial Lab, *White 83* (MO). DARIEN: trail betw Cana and Boca de Cupe, *Stern et al. 619* (MO); vic of Cana, *Stern et al. 692* (MO); Tucute, *Terry & Terry 1397* (MO). LOS SANTOS: vic of Tonosí, *Stern et al. 1867* (MO). PANAMA: San Jose I, *Johnston 758* (GH), *1355* (GH).

6. **Tournefortia cuspidata** H.B.K., Nov. Gen. Sp. Pl. **3:** 83, 1818.—Fig. 6.

T. obscura DC., Prodr. **9:** 517, 1845.

Shrubs, decumbent and liana-like or ± erect to ca 3.5 m, the stems pubescent, the hairs 4-6 mm long, brown. *Leaves* alternate, elliptic, ovate, or rarely obovate or ovate-lanceolate, entire, acuminate, sometimes narrowly so, the bases obtuse, to 18 cm long and 8 cm wide, pubescent on both surfaces, especially on the veins beneath; petioles to ca 2 cm long. *Inflorescences* cymose, densely-flowered, scorpioid, mostly terminal. *Flowers* sessile; calyx of 5 sepals, lanceolate to subulate, densely strigose, ca 5-6(-9) mm long; corolla white to yellow, strigose, the tube ca 6-7 mm long, the lobes ca 2-2.5 mm long, ± keeled; stamens 5, borne halfway up the corolla tube, ± sessile, the anthers ca 1 mm long; ovary ovoid, the style very short or absent, the stigma conical, a swollen ring basally. *Fruit* fleshy, somewhat lobed basally, ca 3-4 mm long, separating into (2-)4 nutlets at maturity.

Central America, the West Indies, and northern South America.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 411* (F); junction of Ríos Changuinola & Terebe, *Lewis et al. 951* (MO); Almirante, nr Dos Nulla, *McDaniel 5138* (MO); Chiriquí Lagoon, Water Valley, *von Wedel 770* (MO), *1282* (MO), *1674* (MO), Old Bank I, *von Wedel 1959* (MO), Little Bocas, *von Wedel 2510* (MO), *2559* (MO). CANAL ZONE: Barro Colorado I, *Aviles 957* (F), *Brown 90* (F), *Woodworth & Vestal* 328 (F), 523 (F). DARIEN: Boca Grande I, *Duke 8843* (MO). PANAMA: E of Pacora, *Woodson et al. 721* (MO), *722* (MO).

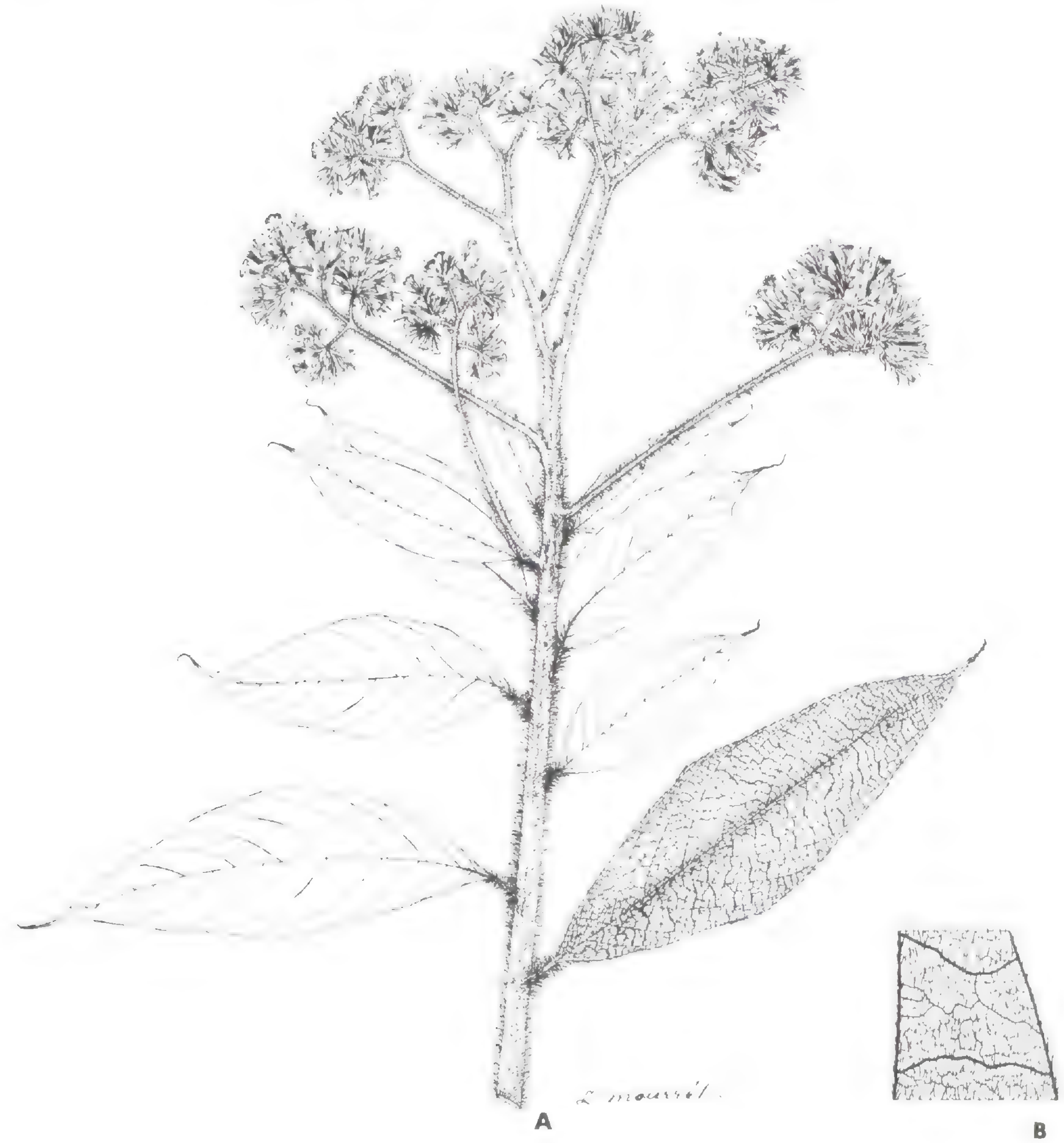

Fig. 6. *Tournefortia cuspidata* H.B.K.: A, habit (ca × ½); B, upper surface of leaf (ca × 4). After *Aviles* 957 (F).

7. **Tournefortia hirsutissima** L., Sp. Pl. 140, 1753.—Fig. 7.

Shrubs, vines, or rarely trees, the stems pubescent, the hairs 1-2 mm long. *Leaves* alternate, elliptic to ovate, acute, sometimes slightly acuminate, entire, the bases weakly rounded to obtuse, to 17 cm long and 8 cm wide, pubescent on both surfaces, frequently scabrous on the upper; petioles ca 0.5-2.5 cm long. *Inflorescences* cymose, scorpioid, axillary or terminal, densely-flowered. *Flowers* sessile; calyx of 5 sepals, ± free, subulate to lanceolate, ca 2-4 mm long, pubescent on both surfaces and sometimes noticeably so on the margins; corolla white, densely strigose above and glabrous near the base, the tube 4.5-5.5 mm long, the lobes ca 2 mm long; stamens 5, sessile, the anthers ca 1 mm long; ovary globose,

Fig. 7. *Tournefortia hirsutissima* L.: A, habit (ca × ½); B, upper surface of leaf (ca × 4.5); C, fruit (ca × 4.5); D, fruit, very pubescent (× 4.5). A-C, after *Allen 4654* (MO); D, after *Tyson 1572* (MO).

the style absent, the stigma stout and conical. *Fruit* pyramidal, yellow-green, ± pubescent, often densely so, ca 5-6 mm high, containing 4 nutlets.

Widely distributed in Central America.

BOCAS DEL TORO: s. loc., *von Wedel 452* (MO). CANAL ZONE: Madden Dam, nr Río Chagres, *Seibert 560* (MO); Barro Colorado I, Gross Point, *Shattuck 970* (MO); Ft San Lorenzo, *Tyson 1572* (MO), *Tyson & Blum 3698* (MO). CHIRIQUI: Llanos on slopes of Volcán de Chiriquí Viejo, *Allen 968* (MO); vic of Boquete, *Allen 4654* (MO). PANAMA: Tocumen, *Dwyer 4056* (MO).

8. **Tournefortia johnstonii** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 991, 1938.

Shrubs, to ca 3 m, stems densely pubescent, the hairs short, brown. *Leaves* opposite to subopposite, ovate to ovate-elliptic, finely undulate to irregularly finely dentate, acute or acute-acuminate, the bases ± obtuse, to 17 cm long and 8 cm wide, densely to moderately short-hairy, more so on the veins beneath, cystolith-dotted; petioles to ca 3 cm long. *Inflorescences* cymose, once or twice dichotomously branched, the branches to ca 12 cm long, axillary or terminal. *Flowers* ± sessile or with pedicels to ca 1 mm long; calyx of 5 free sepals, narrow-lanceolate, 7-10 mm long, strigose; corolla green to yellow, strigose, the tube ca 5-7 mm long, the lobes keeled, each ca 2 mm long; stamens 5, borne near the apex at the corolla tube, sessile, the anthers ca 1.8 mm long; ovary ovoid, the style ca 1-2 mm long, the stigma conical. *Fruit* pyramidal, unlobed, fleshy, ca 5-7 mm in diameter, separating into 1-4 nutlets at maturity.

Apparently occurring only in Costa Rica and Panama.

CHIRIQUI: Volcán de Chiriquí, *Davidson 976* (F), vic of Casita Alta, *Woodson et al. 888* (MO, NY).

Standley, in his Flora of Costa Rica (Publ. Field Mus. Nat. Hist. Bot. Ser. **18:** 991, 992, 1938), described two new species, *T. johnstonii* and *T. ramonensis.* The Panamanian collections cited above have the longer sepals and corolla tubes which Standley attributed to *T. johnstonii.* However, when these specimens are compared with a photo of the type of *T. ramonensis* (*Brenes 6118,* photo GH from F), I have serious doubts about the validity of their separation. I have not seen sufficient material to make this reduction with assurance.

Because of insufficient material, one collection of *Tournefortia* remains unnamed:

Woodson & Schery 609 (MO) (Chiriqui: vic of Bajo Chorro): shrub to 3 m, the branches densely brown-pubescent; leaves ± elliptic, ca 11-14 cm long and 4-5 cm wide, pubescent and cystolith-dotted on both surfaces; sepals lanceolate, ca 5-7 mm long in fruit; style ca 2 mm long, the stigma conical; fruit with a dry exocarp (?), unlobed. This collection may be referable to either *T. johnstonii* or *T. ramonensis,* but the fruit lacks the fleshy exocarp of these species. I am unable to determine if this is only an immature condition in the Woodson & Schery collection. See also the discussion of *T. johnstonii.*

5. BOURRERIA

Bourreria P. Br., Hist. Jamaica 168, 1756.

Trees or shrubs. *Leaves* alternate, rarely almost whorled, simple, mostly lanceolate or elliptic; petiolate. *Inflorescences* cymes, open and many-flowered or occasionally few-flowered. *Flowers* perfect, ± actinomorphic, sessile or pedicellate; calyx

campanulate, closed in bud, 2-5-lobed; corolla funnelform to salverform, 5-lobed, the lobes frequently rounded; stamens 5, included or exserted, borne on the corolla throat, subsessile or the filaments only shortly free, the anthers narrow to broadly oblong; ovary ovoid, unlobed, 2- or incompletely 4-locular, the style bifid near the apex, the stigmas 2 and capitate or peltate. *Fruit* drupaceous, ± spherical, the pericarp thin, enclosing 4 nutlets.

About 30 species, mostly in the West Indies, but a few occur in Venezuela, Central America, and Florida.

a. Corolla tubes ca 17-23 mm long, the lobes ca 9 mm in diam; leaves to 25 cm long . . . . . 1. *B. panamensis*

aa. Corolla tubes < 6 mm long, the lobes ca 4-5 mm in diam; leaves to 16 cm long . . . . . 2. *B. oxyphylla*

1. **Bourreria panamensis** I. M. Johnston, Jour. Arnold Arb. **29:** 229, 1948.

B. superba var. *glabra* Schery, Ann. Missouri Bot. Gard. **29:** 366, 1942.

Trees, to 17 m, glabrous. *Leaves* ovate to obovate, acute, entire, the bases obtuse, to 25 cm long and 10 cm wide, somewhat coriaceous, glabrous; petioles ca 1-2.5 cm long. *Inflorescences* cymose, paniculate and few-flowered, mostly terminal. *Flowers* with pedicels ca 0.5-1.5 cm long; calyx campanulate, coriaceous, glabrous, the tube ca 6-9 mm long, 5-lobed, the lobes deltoid, subequal, and ca 3.5-5.5 mm long; corolla funnelform, white, densely papillose-glandular on both surfaces, the tube ca 17-23 mm long, 5-lobed, the lobes semi-orbicular, ca 8-9 mm deep and 9-10 wide; stamens 5, included, borne on the corolla throat, subsessile, the filaments glabrous, the anthers ca 2.5-3 mm long and 2-2.2 mm wide; ovary subovoid, minute at anthesis, ca 1-2 mm high, the style stout, ca 9-11 mm long, bifid near the tip, the stigmas 2 and peltate. *Fruit* unknown.

Known only from the Chiriquí Lagoon region of Panama.

BOCAS DEL TORO: Chiriquí Lagoon, Colon I, *von Wedel 2472* (MO), *2949* (GH, MO), *2974* (GH).

2. **Bourreria oxyphylla** Standl., Trop. Woods **16:** 40, 1928.—Fig. 8.

Trees, small, the younger branches with sparse appressed pubescence. *Leaves* ± elliptic, acute, entire, the bases obtuse, to 16 cm long and 8 cm wide, ± glabrous on both surfaces; petioles ca 1-1.5 cm long. *Inflorescences* cymose, paniculate, axillary or terminal, the branches softly pubescent. *Flowers* subsessile to peduncles ca 3 mm long; calyx weakly campanulate, softly pubescent, the tube ca 4-5 mm long, 4-5-lobed, the lobes deltoid, subequal, ca 1-1.8 mm long; corolla funnelform, white, softly glandular-pubescent, the tube ca 4.5-5.5 mm long, 5-lobed, the lobes semi-orbicular to obovate, ca 4 mm deep and 5 mm wide; stamens 5, exserted, borne on the corolla throat, the filaments ca 4 mm long, the anthers ca 1.7-1.9 mm long; ovary oblong-ovoid, the style ca 4 mm long, the stigmas 2 and peltate. *Fruit* drupaceous, pyramidal, ca 5-7 mm high, the pericarp hardened.

Apparently known only from British Honduras, Honduras, and Panama.

COLON: beach betw Fató & Playa de Damas, *Pittier 3941* (GH). DARIEN: Chusomocatro & Río Areti, *Duke 8712* (MO). SAN BLAS: Mulatuppu, *Duke 8533* (MO); Soskatupu I, *Duke 8940* (MO).

Fig. 8. *Bourreria oxyphylla* Standley: A, habit (× 5/8); B, flower (× 2). After *Duke 8940* (MO).

6. EHRETIA

Ehretia P. Br., Hist. Jamaica 168, 1756.

Trees or shrubs. *Leaves* alternate, simple, pinnately-nerved, entire or dentate; mostly petiolate. *Inflorescences* paniculate or cymose, mostly terminal. *Flowers* perfect, ± actinomorphic, subsessile to pedicellate; calyx of 5 sepals, open in bud, free or somewhat connate basally; corolla ± funnelform, small, white, 5-lobed, the lobes spreading; stamens 5, mostly exserted, the anthers linear or broadly oblong; ovary 2- or 4-locular, the style bifid near the tip, the stigmas 2, and capitate or clavate. *Fruit* drupaceous, mostly spherical, with one 4-loculed and 4-seeded stone, with two 2-loculed, 2-seeded stones or with 4 separate stones.

Fig. 9. *Ehretia austin-smithii* Standley: A, habit (× 5/6); B, fruit (ca × 2). After *White 220* (F).

About 40 species, mostly in the Old World tropics, with a few in the West Indies and Central America.

The wood is of economic value in some of the tree species.

1. **Ehretia austin-smithii** Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 984, 1938.—Fig. 9.

Trees, to 25 m, the younger branches pubescent. *Leaves* ± ovate, acute, serrate, the bases rounded, or shallowly truncate, to 6 cm long and 5 cm wide, ± scabrous above and sparsely pubescent beneath; petioles to ca 1 cm long. *Inflorescences* cymose, arranged in an open panicle, mostly terminal, the branches scurfy. *Flowers* subsessile to pedicels ca 1-2 mm long; calyx of 5 sepals, connate

basally, open in bud, ca 1.6-1.8 mm long over-all, the lobes ovate, the margins fimbriolate; corolla ± campanulate, white, the tube ca 1.8-2 mm long, 5-lobed, the lobes ovate, ca 1.2-1.4 mm long; stamens 5, exserted, borne low in the corolla throat, the filaments ca 1.6-1.8 mm long, glabrous, the anthers ca 1 mm long; ovary ovoid, the style stout, ca 1 mm long, very shortly bifid, the stigmas 2 and recurved. *Fruit* drupaceous, white to green, ± ovoid, ca 10-12 mm in diam.

Apparently occurring only in Costa Rica and Panama.

CHIRIQUI: Río Chiriquí Viejo Valley nr Bambito Woods, *White 220* (F).

The above collection is in fruit only; the floral description was completed from Costa Rican material [*Austin Smith H528* (MO, isotype)].

7. CORDIA

Cordia L., Sp. Pl. 190, 1753.

Shrubs, sometimes scandent, or trees, sometimes functionally dioecious, strigose to softly pubescent, the hairs simple, uniseriate, or stellate. *Leaves* mostly alternate, rarely subopposite, simple, mostly homomorphic, sometimes dimorphic, petiolate. *Inflorescences* cymes, very irregular, paniculate and open, spike-like, or rarely densely glomerate, axillary or terminal, the bracts generally absent. *Flowers* perfect and homomorphic or functionally unisexual and slightly heteromorphic, actinomorphic, ± sessile; calyx of 5 connate sepals, tubular or ± campanulate, sometimes costate, densely strigose to softly pubescent, sometimes with resinous dots when young, 5-lobed or splitting irregularly and 2-4-lobed; corolla of 5(-12) connate petals, funnelform to salverform, marcescent or falling soon after anthesis, sparsely strigose to glabrous, white to cream, 5(-12)-lobed, the lobes oblong and conspicuous, almost as broad as long, or shallow and obscure; stamens as many as the corolla lobes, functional, or reduced and abortive, epipetalous, borne on the corolla throat, alternate, the filaments sometimes fimbriolate and/or hooked near the base, the anthers dehiscing longitudinally, introrse; ovary 4-loculed, functional or reduced and abortive, unlobed, the ovules 1-4, usually only one developing, style slender, elongate, twice bifid, the stigmas 4 and capitate or clavate. *Fruit* usually drupaceous, unlobed, the exocarp dry or mucilaginous; seed usually 1.

A genus of about 200 species, distributed in the warmer regions of the world. Seventeen species are found in Panama.

a. Inflorescences open paniculate cymes, repeatedly branched; corolla lobes readily delimited.
  b. Flowers functionally dioecious, heteromorphic, sometimes only slightly so; stamens reduced in ♀ flowers, the style reduced in ♂ flowers.
    c. Calyx costate; leaves homomorphic ..... 1. *C. diversifolia*
    cc. Calyx not conspicuously costate; leaves large and heteromorphic, some ± ovate, the others much smaller and ± orbicular ..... 2. *C. panamensis*
  bb. Flowers perfect, homomorphic; stamens and style fully developed.
    d. Hairs stellate ..... 3. *C. alliodora*
    dd. Hairs simple.
      e. Leaves conspicuously bullate ..... 4. *C. duyeri*
      ee. Leaves not bullate.

f. Corolla-lobes broader than long; leaves ovate to obovate and ± toothed on the distal portion ..... 5. *C. dentata*
ff. Corolla-lobes not broader than long; if leaves ovate or obovate, then not ± toothed on the distal portion.
g. Calyx persistent, enveloping the maturing fruit; corolla vermillion; leaves large and coarsely scabrous ..... 6. *C. sebestena*
gg. Calyx persistent, but not enveloping the maturing fruit; corolla white or cream; leaves not conspicuously large and scabrous.
h. Branching noticeably dichotomous; veins and veinlets of under surface of leaves covered by appressed slender hairs which cover and converge over the veinlet-areoles ..... 7. *C. bicolor*
hh. Branching not regularly dichotomous; undersurface of leaves glabrous or pubescent but not with veins and veinlets of undersurface of leaves covered by appressed slender hairs which cover and converge over the veinlet-areoles.
i. Leaves ± obovate, conspicuously and abruptly long acuminate; branches of the inflorescence essentially glabrous ..... 8. *C. lasiocalyx*
ii. Leaves ovate to elliptic-lanceolate, acuminate but not abruptly so; branches of the inflorescence softly pubescent.
j. Leaves rigid, noticeably falcate; calyx ca > 7 mm long ..... 9. *C. protracta*
jj. Leaves not conspicuously rigid or falcate; calyx < 6 mm long.
k. Leaves ± ovate, drying brown-black; calyx ca 3-4 mm long; corolla-lobes ca 2 mm long ..... 10. *C. lucidula*
kk. Leaves ± lanceolate-elliptic, appearing gray-green above; calyx 5.5-6 mm long; corolla-lobes ca 5 mm long ..... 11. *C. porcata*

aa. Inflorescences densely glomerate, sometimes bifid, or spicate; corolla-lobes frequently so shallow as to be obscure.
l. Inflorescences bifurcate cymes, each branch terminating in a small head of flowers ..... 12. *C. bifurcata*
ll. Inflorescences glomerate, or elongate and spike-like.
m. Inflorescences glomerate.
n. Calyx-lobes ± deltoid, < 1 mm long.
o. Inflorescences axillary; petioles ca 1-4 mm long ..... 13. *C. lineata*
oo. Inflorescences internodal or terminal; petioles ca 5-10 mm long ..... 14. *C. inermis*
nn. Calyx-lobes caudate, ca 2-4 mm long ..... 15. *C. globosa*
mm. Inflorescences spike-like.
p. Bases of petioles decurrent on the axillary peduncles for 5-10 mm; inflorescences axillary ..... 16. *C. spinescens*
pp. Bases of petioles not decurrent on axillary peduncles; inflorescences mostly terminal or sometimes internodal ..... 17. *C. curassavica*

1. **Cordia diversifolia** Pavon ex DC., Prodr. **9**: 474, 1845.

C. johnstonii Cufodontis, Arch. Bot. Sist. **10**: 41, 1934.
C. petensis Lundell, Wrightia **4**: 49, 1968.

Shrub or tree, to 10 m, functionally dioecious, branchlets densely soft-pubescent. *Leaves* alternate, lanceolate-elliptic, entire or sometimes sparsely dentate near the apices, acute to acute-mucronate, the bases obtuse to slightly oblique, to

20 cm long and 7 cm wide, roughly-pubescent, especially on the upper surface. *Inflorescences* cymes, ± paniculate, the tips scorpioid, terminal, ca 15 cm long, softly-pubescent. *Flowers* functionally unisexual, ± sessile. *Staminate flowers* with the calyx tubular, ca 4-5 mm long, ca 5-dentate, conspicuously ca 10-ribbed, pubescent; corolla white, the tube ca 4-5 mm long; the lobes oblong, ca 2-3 mm long and 1-1.2 mm wide; stamens 5, exserted, the filaments sparsely pubescent near the base, ca 4 mm long, the anthers ca 1.6-1.8 mm long; ovary reduced and abortive, the style absent. *Pistillate flowers* with the calyx tubular, ca 4-5 mm long, 4-5-dentate, weakly ribbed, pubescent; corolla white, the tube ca 4 mm long, the lobes oblong, ca 2 mm long and < 1 mm wide; stamens ca 5, reduced and abortive, weakly exserted, the filaments ca 1 mm long, glabrous, the anthers ca 0.5 mm long; ovary ovoid, the style well-developed and exserted, the branches elongate, ca 4 mm long in late flowering. *Fruit* ellipsoidal, fleshy, ca 7-9 mm long, the calyx persistent and saucer-shaped.

Central America.

BOCAS DEL TORO: Almirante, rd to the "Bomba", *Blum 1314* (MO); Changuinola, to 5 mi S of junction of Ríos Changuinola & Terebe, *Lewis et al. 795* (MO), *937* (MO), *946* (MO); Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1994* (MO); vic of Chiriquí Lagoon, *von Wedel 1070* (MO), Old Bank I, *von Wedel 1894* (GH), *2051* (MO), Pumpkin R., *von Wedel 2580* (MO), *2595* (MO), Water Valley, *von Wedel 2745* (MO); vic of Nievecita, *Woodson et al. 1824* (F, MO).

2. **Cordia panamensis** Riley, Kew Bull. **1927:** 135, 1927.

Shrubs or trees to 15 m, functionally dioecious, strigose. *Leaves* alternate or subopposite, dimorphic, the larger ovate to ovate-elliptic, acute, ± entire to rarely finely dentate, the bases rounded, ± oblique or rarely obtuse, to 30 cm long and 15 cm wide, the smaller fewer in number, subopposite the larger, ovate-orbicular, acute, entire, the bases rounded and < half the size of the larger, scabrous or strigose on the upper surface, tomentose or strigose beneath; petioles, ca 5-15 mm long, strigose. *Inflorescences* cymes, paniculate, mostly terminal or borne in the dichotomous axils of the branches, to ca 15 cm long and wide. *Flowers* functionally unisexual, ± sessile. *Staminate* flowers subglobose in bud; calyx campanulate, ca 4 mm long, 5-dentate, faintly ribbed, pubescent on both surfaces; corolla ± campanulate, white, the tube ca 3 mm long, the lobes oblong, ca 2 mm long and ca 1.2 mm wide; stamens conspicuously exserted, the filaments ca 3-4 mm long, pubescent basally, the anthers ca 1 mm long; ovary reduced and abortive, the style somewhat developed, included, branched, each branch bifid near the apex. *Pistillate flowers* clavate-cylindric in bud; calyx tubular-campanulate, ca 4 mm long, 5-dentate, 5-ribbed, pubescent on both surfaces, becoming saucer-shaped in fruit; corolla salverform, white, the tube ca 2.5-3 mm long, the lobes oblong, ca 1 mm long and 1 mm wide; stamens 4-5, reduced and abortive, subsessile to filaments ca 1 mm long, glabrous, the anthers ca 0.4-0.5 mm long; ovary ovoid-oblong, the style well-developed, exserted, branched, each branch bifid near the apex, the lobes clavate and recurved. *Fruit* a drupe, ovoid, white to green, black to dark brown on drying, glabrous, ca 6-9 mm long, coriaceous.

Central America, from El Salvador to Panama, and probably in Colombia and Ecuador.

CANAL ZONE: RR tracks along rd to Tropic Test Center, *Correa 261* (MO); Farfan Beach area, *Dwyer 6766* (MO), *Tyson 1823* (MO); Barro Colorado I, Miller Point, *Shattuck 1155* (MO); Albrook A.F.B., *Tyson 1114* (MO); Curundu, nr Survival School, *Tyson 4174* (MO); vic of Miraflores, *White 134* (MO). COCLE: Hills S of El Valle de Antón, *Allen 2481* (MO); Río Hato airstrip, *Blum & Dwyer 2471* (MO). COLON: Nuevo Chagres, beach and adj rdside, *Lewis et al. 1858* (MO). CHIRIQUI: E of Gualaca, *Allen 5032* (MO); 2 mi SW Guabala, *Tyson et al. 4247* (MO). DARIEN: 2 mi E of Santa Fé, *Tyson et al. 4676* (MO). PANAMA: San José I, *Andersson s.n.* (MO), *Erlanson 226* (GH), *276* (NY); Cerro Campana, *Duke 8667* (MO); Pedro Gonzales I, *Dwyer 1705* (MO); E of Pacora, *Woodson et al. 757* (MO); Taboga I, *Woodson et al. 1544* (MO), *1547* (MO). SAN BLAS: Mulatuppu, *Duke 8540* (MO); Ailigandi, *Dwyer 6827* (MO). VERAGUAS: Coiba I, *Dwyer 1574* (MO), *2343* (MO); Santiago, 4 mi from Transisthmian Hwy, *Dwyer & Kirkbride 7412* (MO).

Cordia panamensis is one of the more perplexing species in this difficult genus. Other species (*Cordia macrophylla* L., *C. sulcata* DC.) also have large dimorphic leaves and indistinguishable flowers and fruits. Johnston (Jour. Arnold Arb. **30:** 126, 1949) maintained their separation on the basis of geographical range and vegetative characters, but admitted that *C. macrophylla, C. panamensis,* and *C. sulcata* were closely related and were not "strong" species. From his key, and from the fact that their geographical ranges do tend to overlap, as well as from an examination of large numbers of Panamanian collections (whose vegetative characters are ambiguous and exhibit continuous variation), it appears that this group may well represent a polymorphic species centering in the West Indies and Central America.

To add to the above confusion, fruiting specimens of *C. panamensis* look suspiciously similar to those of *C. stellifera* I. M. Johnston, the species name of which refers to the star-like appearance of the calyx in fruit. This latter species is perfect-flowered and, although it does not appear to be in Panama (I have not seen large-leaved, perfect-flowered specimens of *Cordia* from that country), the question can be raised concerning the identification of fruiting collections of *"C. stellifera"* from other localities: are these in fact female specimens of *C. panamensis,* since both have a star-like calyx in fruit?

3. **Cordia alliodora** (Ruiz & Pav.) Cham., Linnaea **8:** 121, 1833.

Cerdona Alliodora Ruiz & Pav., Fl. Peru. **2:** 47, *pl. 184,* 1799.

Trees, to 20 m, stems and branches with stellate hairs, nodes swollen and inhabited by ants. *Leaves* alternate, ovate-elliptic, occasionally ovate, entire, acute or acute-mucronate, the bases obtuse or oblique, to 18 cm long and 8 cm wide, sparsely to densely covered with stellate hairs, especially on the undersurface; petioles to ca 3.5 cm long. *Inflorescences* irregular cymes, spreading and loose, or sometimes compacted, the primary panicles to 18-20 cm long. *Flowers* perfect, ± sessile or with pedicels to ca 1 mm long; calyx tubular, ca 4-5 mm long, densely soft-pubescent, ca 10-ribbed and with 5 small teeth; corolla-tube cylindrical, ca 3 mm long, lobes 5, spreading, each ca 5-6 mm long, white to cream, somewhat hirsute at the throat, ± persistent; stamens 5 (rarely more), borne at the corolla throat, the filaments ca 5-6 mm long at maturity, each with a hooked fimbriolate

base, the anthers ca 1.5-1.8 mm long; ovary cylindrical, ca 1 mm long, ribbed or wrinkled, the style elongate, 3-4 mm long, the stigmas 4, as a result of 2 divisions, each < 1 mm long. *Fruit* cylindrical, not drupaceous, the pericarp fibrous and chartaceous, ca 5-6 mm long.

Widely distributed in tropical America.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Old Bank I, *von Wedel 1877* (MO). CANAL ZONE: vic of Gorgas Hospital, *Blum 2210* (MO); Tropic Test Center, *Dwyer & Robyns 56* (MO); Government Forest along Las Cruces Trail, *Hunter & Allen 449* (MO, NY); Chiva-Chiva Trail, Red Tank to Pueblo Nueve, *Piper 5755* (NY). COLON: Juan Mina, Río Chagres, *Allen 4198* (MO). HERRERA: vic of Ocú, hill above cantera of Sr. Joaquan Carrizo, *Stern et al. 1721* (MO). LOS SANTOS: vic of Tonosí, Guanico, *Stern et al. 1856* (MO).

4. **Cordia dwyeri** Nowicke, Phytologia (in press).—Fig. 10.

Shrubs, to 3.5 m, the stems densely pubescent, the hairs simple, brown. *Leaves* ovate, sometimes ± obovate, acuminate, revolute, the bases ± rounded, to 31 cm long and 13 cm wide, sparsely pubescent above, densely pubescent beneath, coriaceous and conspicuously bullate; petioles 1-2 cm long, stout, pubescent. *Inflorescences* cymose, paniculate, densely flowered, the branches pubescent. *Flowers* perfect (?), ± sessile; calyx cupulate, densely strigose, the tube ca 4-5 mm long, 3-4-lobed, the lobes deltoid and ca 1.5-2 mm long; corolla salverform, color unknown, the tube 4-5 mm long, 5-lobed, the lobes oblong, 2.5-3 mm long and 2-2.5 mm wide; stamens 5, exserted, the filaments ca 7-8 mm long, pubescent basally, the anthers ca 1.5 mm long; ovary ovoid, the style ca 1.2 mm long, the stigmas clavate. *Fruit* unknown.

Apparently only from Panama.

COLON: Santa Rita Ridge, 19 km from Transisthmian Hwy, *Dwyer 8857* (holotype MO; isotypes F, GH).

The bullate condition of the leaves readily separates *C. dwyeri* from all other Panamanian species of *Cordia.*

5. **Cordia dentata** Poir., Encyc. **7:** 48, 1806.

Shrubs, or trees to 25 m, coarsely pubescent. *Leaves* alternate, ovate to obovate, sparsely mucronate-dentate, blunt-acute (slightly mucronate), the bases obtuse to rounded, to 12 cm long and 7 cm wide, coarsely pubescent, the hairs with multicellular bases; petioles to 2 cm long. *Inflorescences* irregular panicles, the apices scorpioid, ca 10-13 cm long and wide, terminal. *Flowers* perfect, ± sessile; calyx tubular, ca 10-ribbed, 3-4 mm long, 3(-5)-lobed, sparsely strigose on the ribs; corolla white to cream, funnelform, the tube ca 3-4 mm long with 5 widely spreading lobes 6-8 mm long, glabrous; stamens 5, borne on the corolla throat, the free filament 3-4 mm long, sparsely strigose at the point of attachment, the anthers ca 1.7-1.9 mm long; ovary bottle-shaped, the style ca 2-3 mm long, divided and the branches redivided near the apices, the stigmas 4. *Fruit* ovoid, with fleshy exocarp and bony endocarp, white, to 1.5 cm long.

Mexico, Central America, the West Indies, and northern South America.

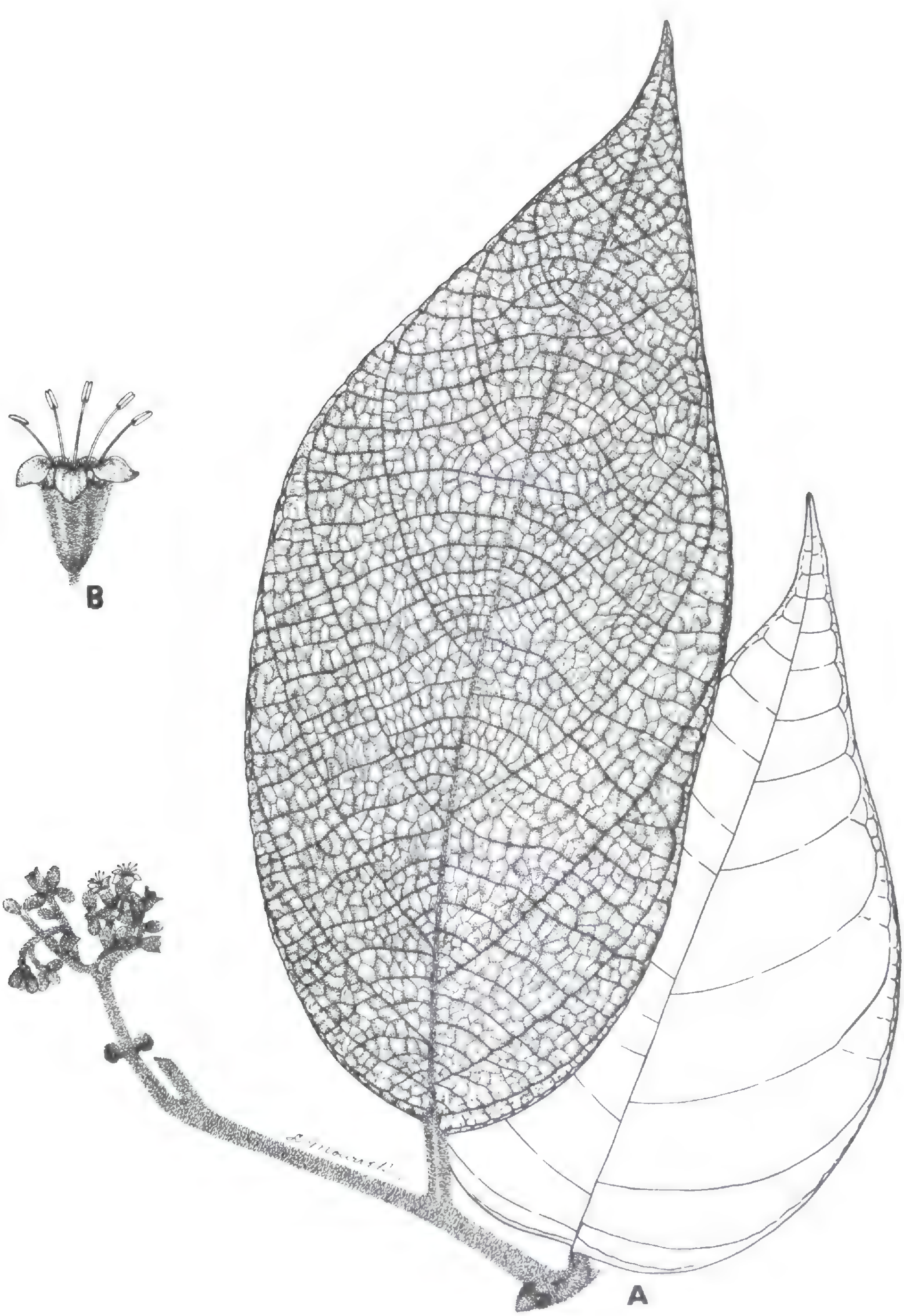

Fig. 10. *Cordia dwyeri* Nowicke: A, habit (ca × ½); B, flower (ca × 2). After *Dwyer* 8857 (MO).

HERRERA: vic of Pesé, *Allen 805* (MO, NY). LOS SANTOS: vic of Las Tablas, *Duyer 1167* (MO); Monagre Beach, *Duyer 4165* (MO). VERAGUAS: 5 mi E Santiago, *Tyson et al. 4289* (MO).

This is the "*Cordia alba*" of most authors.

6. **Cordia sebestena** L., Sp. Pl. 190, 1753.

Shrubs or trees, the younger stems pubescent. *Leaves* ovate, sometimes broadly so, acute, entire, the bases ± rounded, to 21 cm long and 15 cm wide, scabrous above, pubescent on the veins beneath; petioles ca 3-4 cm long. *Inflorescences* cymose, paniculate, loosely-flowered. *Flowers* perfect, pedicels ca 0.5-1.5 cm long, pubescent; calyx cylindrical, the tube ca 10-12 mm long at anthesis, 3(-4)-lobed, the lobes deltoid and ca 1-2 mm long, greatly enlarging in fruit; corolla funnelform, vermillion, the tube ca 20-25 mm long, 5-6-lobed, the lobes ca 10 mm long and 8-9 mm wide; stamens 5(-6), included, the filaments free from the corolla tube for ca 2-3 mm, ± glabrous at the point of attachment, the anthers ca 2.2-2.4 mm long; ovary ovoid, the style ca 20-25 mm long, the lobes clavate and flattened. *Fruit* drupaceous, ovoid, hard, ca 2-2.5 cm in diam, the calyx tightly adhering and becoming white and fleshy.

Native to the West Indies and ranging from the Bahamas to northern Venezuela.

SAN BLAS: Soskatupu I, *Duke 8963* (MO), *15476* (MO), *Elias 1698* (MO).

This species, which is widely cultivated in the tropics, is very distinctive among the Panamanian members of *Cordia* because of the showy flowers and the large fruit with its adherent calyx. The collections cited above, which are in bud or late-flower-early-fruiting stage, were not adequate for a complete description, so West Indian material [*Wilson 7912* (MO); *Stimson 4200* (MO)] was also utilized.

7. **Cordia bicolor** DC., Prodr. **9:** 485, 1845.

C. trichostyla Pittier, Contr. U.S. Nat. Herb. **18:** 252, 1917.

Trees, 10-20 m, the younger branches and stems appressed-pubescent. *Leaves* elliptic to ovate, acuminate or sometimes acute, entire, the bases obtuse, to 18 cm long and 8 cm wide, darker with appressed pubescence above, paler with slender appressed hairs below that are borne on the veins and veinlets and converge and cover the veinlets-areoles; petioles ca 0.5 cm long. *Inflorescences* cymes, paniculate and ± open. *Flowers* perfect; calyx tubular-campanulate, ca 4 mm long, 5-dentate, the teeth ± unequal, unribbed, pubescent; corolla salverform, white, the tube ca 3-4 mm long, the lobes oblong, ca 1.5-1.7 mm long and ca 1.2 mm wide; stamens exserted, the filaments ca 3 mm long, fimbriolate basally, the anthers ca 1.5-1.6 mm long; ovary ovoid, the style well-developed, the lobes exserted and clavate. *Fruit* a drupe, ovoid, ca 1 cm long, dull green, pubescent with minute grey hairs.

Sporadically distributed in Central America, the southernmost West Indies, and northeastern South America.

CANAL ZONE: Barro Colorado I, *Oppenheimer* 252 (MO). PANAMA: San José I, *Johnston* 620 (GH), 621 (GH), 963 (GH); Altos del Río Pacora, edge of river and cloud forest, *Lewis et al.* 2267 (MO).

Described at various times by Johnston (Jour. Arnold Arb. **21:** 350, 1940; Sargentia **7:** 255, 1949) as being perfect-flowered and functionally unisexual, the plants examined from Panama appear to be perfect-flowered: normal sized stamens and enlarging ovaries are found in the same flower.

8. **Cordia lasiocalyx** Pittier, Contr. U.S. Nat. Herb. **18:** 251, 1917.—Fig. 11A.

Trees, small or medium sized, glabrous. *Leaves* elliptic to obovate, conspicuously and abruptly long-acuminate (apices 1.5-3 cm long), entire, the bases obtuse, to 14 cm long and 5 cm wide, glabrous on both surfaces, chartaceous; petioles ca 0.5-1 cm long. *Inflorescences* cymes, paniculate, axillary or terminal,

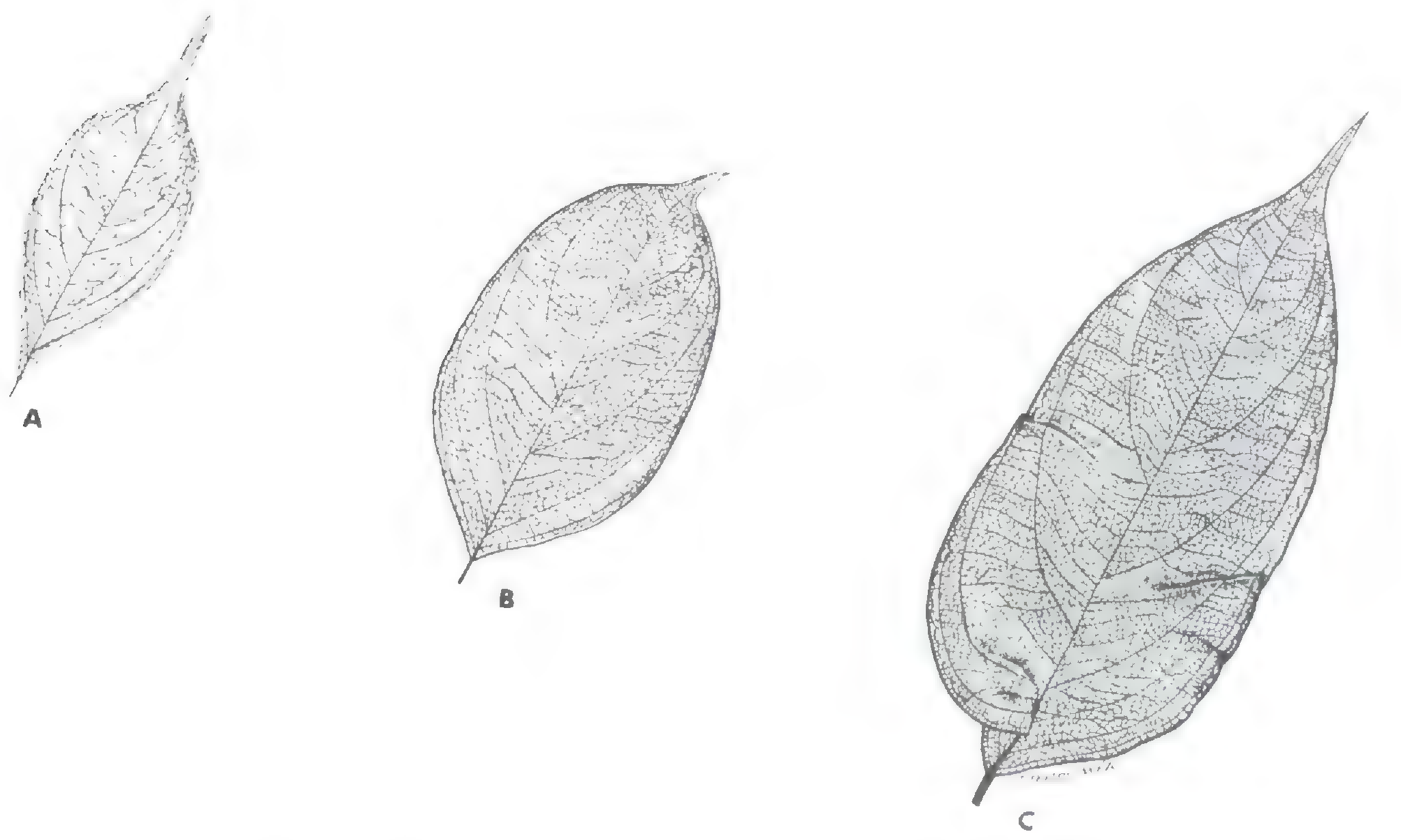

Fig. 11. *Cordia lasiocalyx* Pittier: A, leaf (ca × 3/8), after *Shattuck* 813 (F). C. *lucidula* I. M. Johnston: B, leaf (ca × 3/8), after *Dunlap* 322 (F). C. *protracta* I. M. Johnston: C, leaf (ca × 3/8), after *Cooper* 244 (GH).

the branches glabrous. *Flowers* perfect, ± sessile; calyx cupulate, glabrous, ca 2.5-3 mm long, 3-lobed, the lobes deltoid and ca 2 mm long; corolla funnelform, white, the tube ca 4.5-5.5 mm long, 5-lobed, the lobes oblong, ca 4 mm long and ca 2.2 mm wide; stamens 5, exserted, the filaments ca 3-3.5 mm long, slightly pubescent basally, the anthers ca 1.3-1.5 mm long; ovary ovoid, the style slender, the stigmas clavate. *Fruit* irregularly ovoid, the stylar scar laterally placed, ca 5-6

mm high and ca 9-10 mm wide, color unknown.

Known only from Panama.

CANAL ZONE: Barro Colorado I, Dock area, *Shattuck 813* (F, MO), Gross Point, *Shattuck 853* (F, MO), nr Termite House on shore, *Wilson 69* (F). DARIEN: around Garachine, *Pittier 5694* (holotype US); forests around Pinogana, *Pittier 6560* (US).

The collections cited above have been identified as *Cordia nitida* Vahl, which Johnston (1940) considers as restricted to the West Indies. I am inclined to agree with him after an examination of the West Indian material at the Missouri Botanical Garden. Among the Panamanian species of *Cordia* it is very distinctive because of the leaves: relatively uniform in size and shape with the apices conspicuously acuminate. I have seen only one fruiting specimen, but the drupe appears to mature asymmetrically, with the stylar scar becoming laterally placed.

See also the discussion of *C. protracta*.

9. **Cordia protracta** I. M. Johnston, Jour. Arnold Arb. **21:** 349, 1940.—Fig. 11C.

Shrubs, erect, the young stems softly pubsecent, the mature stems sparsely so. *Leaves* oblong-ovate, acuminate, entire, the bases rounded to ± obtuse, to 22 cm long and ca 10 cm wide, sparsely pubescent on the veins of both surfaces, coriaceous, noticeably falcate: petioles ca 0.5-1 cm long. *Inflorescences* cymes, paniculate, axillary or terminal, the branches softly pubescent. *Flowers* perfect, ± sessile, the buds clavate, ca 6-7 mm long; calyx ± tubular at anthesis, ca 6.5-7.5 mm long, sparsely strigose within and without, 5-lobed, the lobes deltoid and ca 1 mm long; corolla funnelform, white, the tube ca 7-8 mm long, 5-lobed, the lobes oblong, ca 3-4 mm long and 1.6-2 mm wide; stamens 5, exserted, the filaments ca 3-4 mm long, pubescent at the bases, the anthers ca 2 mm long; ovary elongate-ovoid, the style ca 7 mm long, the lobes slender. *Fruit* a drupe, ± ovoid, ca 1 cm long, white.

Panama.

SAN BLAS: Perme, *Cooper 235* (US), *244* (holotype GH; isotype US).

Several Panamanian species of *Cordia* have acuminately-tipped leaves as one of the more conspicuous characters of identification. They are also closely allied in floral characters, but, after an examination of type material, I think that they are all distinct species. *Cordia lasiocalyx* has the most obviously acuminate condition, but its regular and relatively small and thin leaves make it easily separable; *C. protracta,* with its large, rigid and noticeably falcate leaves, provides a striking contrast to *C. lasiocalyx;* the leaves of *C. lucidula* are admittedly intermediate between the above-mentioned conditions, but this species is still easily distinguishable, especially when the pubescence of the inflorescence and floral size are also considered.

10. **Cordia lucidula** I. M. Johnston, Jour. Arnold Arb. **21:** 352, 1940.—Fig. 11B.

Trees, small, to ca 8 m, mostly glabrous, the young stems softly-pubescent. Leaves ovate, sometimes ovate-elliptic or elliptic-lanceolate, acuminate, entire, the

bases obtuse, to 16 cm long and 8 cm wide, ± glabrous on both surfaces, or very sparsely pubescent on the veins beneath, somewhat falcate; petioles ca 0.5-1 cm long. *Inflorescences* cymes, paniculate, open, mostly terminal, the branches softly-pubescent. *Flowers* perfect, ± sessile; calyx cupulate, very sparsely pubescent within and without, ca 2.5 mm long, 3-4-lobed, the lobes deltoid and ca 1 mm long; corolla campanulate, white, the tube ca 4 mm long, 5-lobed, the lobes oblong, ca 2 mm long and ca 1.2 mm wide; stamens 5, exserted, the filaments ca 3.5-4 mm long, pubescent basally, the anthers ca 1.2 mm long; ovary ovoid, the stigmas slenderly clavate. *Fruit* unknown.

Panama and Costa Rica.

BOCAS DEL TORO: Daytonia Farm, *Cooper* 372 (F); Research Lagoon, *Cooper* 406 (F); Changuinola Valley, Potrero I, *Dunlap* 284 (US; holotype, F; isotype), 322 (F); Changuinola Valley, *Dunlap* 356 (F); Chiriquí Lagoon, Fish Creek Hills, *von Wedel* 2425 (MO).

See discussion of C. *protracta*.

11. **Cordia porcata** Nowicke, Phytologia (in press).—Fig. 12.

Shrubs, to ca 3 m, the younger branches softly-pubescent. *Leaves* alternate, elliptic, acuminate, entire, the bases obtuse, to 24 cm long and 9 cm wide, ± rigid, slightly falcate, ± glabrous and grey-green above, sparsely pubescent beneath; petioles ca 2-10 mm long. *Inflorescences* cymes, loosely-flowered, the peduncles softly-pubescent. *Flowers* perfect, ± sessile; buds clavate; calyx cupulate, the tube ca 4 mm long, glabrous, 3-4-lobed, the lobes deltoid, ca 1.5-2 mm long; corolla salverform, white, the tube ca 4-4.5 mm long, 5-lobed, the lobes oblong, ca 5 mm long and ca 1.8 mm wide; stamens 5, exserted, the filaments ca 3-4 mm long, pubescent basally, the anthers ca 2 mm long; ovary ovoid, the style ca 4 mm long at anthesis. *Fruit* obliquely ellipsoidal, 10-12 mm high, apex acute.

Known only from Panama.

COLON: Santa Rita Ridge lumber rd, *Correa & Dressler* 742 (MO), *1076* (holotype MO); Santa Rita Ridge, 19 km from Transisthmian Hwy, *Dwyer* 8581 (MO), hwy to 8 mi E, *Dwyer et al.* 9027 (MO). LOS SANTOS: Cerro Pilón, *Dwyer & Lallathin* 8586 (MO).

12. **Cordia bifurcata** Roem. & Schult., Syst. Veg. **4:** 466, 1819.—Fig. 13.

Shrubs, small, the stems strigose. *Leaves* ovate to elliptic, ± acuminate, entire, the bases obtuse, to 10 cm long and 4 cm wide, sparsely pubescent on the upper surface, more so on the lower surface; petioles ca 3-10 mm long. *Inflorescences* cymes, the branches very reduced, sometimes appearing as a capitulum in bud, terminal or internodal. *Flowers* perfect, sessile; calyx cupulate, strigose, ca 1.8-2 mm long (4-)5-lobed, the lobes shallowly deltoid; corolla weakly campanulate, white, ca 3 mm long, obscurely 5-lobed, the lobes very small; stamens 5, weakly exserted if at all, the filaments ca 1 mm long, pubescent basally, the anthers ca 0.5 mm long; ovary ovoid, the style ± included. *Fruit* drupaceous, ± ovoid, enclosed within the calyx, ca 2-3 mm long.

Costa Rica, Panama, and southward along the Andes.

Fig. 12. *Cordia porcata* Nowicke: A, habit (× ½); B, flower (ca × 3); C, fruit (ca × 2). After *Correa & Dressler 1076* (MO).

BOCAS DEL TORO: Almirante, Research Grounds, *Cooper* 83 (F, GH, NY); Changuinola Valley, *Dunlap* 90 (GH). DARIEN: vic of Paya, Río Paya, *Stern et al.* 268 (GH).

13. **Cordia lineata** (L.) Roem. & Schult., Syst. Veg. **4:** 464, 1819.—Fig. 14. *Varronia lineata L.*, Syst. Nat. ed. 10, 916, 1759.

Shrubs, scandent, or small trees, softly-pubescent. *Leaves* alternate, elongate-elliptic to elongate-ovate, coarsely dentate, acute to ± acuminate, the bases rounded to obtuse, to 12 cm long and 4 cm wide coarsely pubescent; ± sessile to petioles 3-4 mm long. *Inflorescences* cymes, densely glomerate, mostly axillary,

Fig. 13. *Cordia bifurcata* Roem. & Schult.: habit (ca × 5/6). After *Stern et al.* 268 (GH).

Fig. 14. *Cordia lineata* (L.) Roem. & Schult.: habit (ca × 5/8). After *Duke* 5580 (MO).

the peduncles to 4.5 cm long. *Flowers* perfect, sessile; calyx cupular, 2-3 mm long, densely strigose, 5 small teeth; corolla tubular, white, ca 3-4 mm long, with 5 inconspicuous lobes; stamens 5, borne on the corolla throat, the filaments ca < 1 mm long, the anthers ca 0.5-0.7 mm long; ovary globose, the style slender, ca 1.5-2 mm long, forked, the branches redivided near the apices, the stigmas 4. *Fruit* a drupe, red, enveloped by the calyx, ca 3-4 mm long.

Mexico, Central America, the northern West Indies, and possibly northern South America.

DARIEN: Chepigana, *Duke & Bristan 264* (MO). PANAMA: PanAmerican Hwy at Río Mamonica, *Duke 5580* (MO); forests bordering grasslands on Cerro Campana, *Duke 8677* (MO); betw Pacora & Chepo, boggy grasslands & marginal thickets, *Woodson et al. 1671* (MO). SAN BLAS: Mulatupo, Río Ibedi, *Cooper 276* (NY), *Duke 8487* (MO); Río Mulatupo headwaters, *Elias 1742* (MO); mouth of Río Ailigandí to 2.5 mi inland, *Lewis et al. 204* (MO).

14. **Cordia inermis** (Mill.) I. M. Johnston, Jour. Arnold Arb. **30:** 95, 1949.— Fig. 15.

Lantana inerma Mill., Gard. Dict. 1768.
Cordia cana Mart. & Gal., Bull. Acad. Roy. Soc. Bruxelles 11(2): 331, 1844.

Shrubs, to 2 m, the younger stems scabrous, the mature stems less so. *Leaves* ovate, acute-acuminate, serrate or doubly serrate, the bases entire, ± rounded and slightly attenuate, to 9 cm long and ca 3-4 cm wide, sparsely scabrous on both surfaces; petioles ca 0.5-1 cm long. *Inflorescences* cymose, appearing as dense capitula, 5-7 mm wide, terminal or internodal, the peduncles slender, pubescent, < 3 cm long. *Flowers* perfect, sessile; calyx cupulate, strigose, ca 1.8 mm long, 5-lobed, the lobes deltoid; corolla weakly campanulate, white, the tube ca 2.5-3.5 mm long, obscurely 5-lobed, the lobes ca 0.4 long and 0.6 mm wide; stamens 5, slightly exserted, the filaments ca 1 mm long, pubescent basally, the anthers ca 0.5 mm long; ovary semi-spherical, style not exserted. *Fruit* unknown.

Mexico, Central America, and the north coast of Colombia.

PANAMA: Taboga I, *Woodson et al. 1478* (F, GH).

Johnston (Jour. Arnold Arb. **30:** 95, 1949) also reports this species from Taboga Island. The specimen cited [*Standley 27039* (US)] has not been seen.

15. **Cordia globosa** (Jacq.) H.B.K., Nov. Gen. Sp. Pl. **3:** 76: 1818.

Varronia globosa Jacq., Enum. 14, 1760.

Shrubs, erect, 1-2 m, the stems scabrous. *Leaves* ovate, sometimes broadly so, acute, serrate, the bases rounded to obtuse and ± oblique, to 6 cm long and 5 cm wide, scabrous on both surfaces; petioles ca 0.5-1.5 cm long. *Inflorescences* cymose, appearing as dense capitula, ca 1 cm in diam, the peduncles slender, scabrous, ca 1-2 cm long. *Flowers* perfect, sessile; calyx cupulate, ca 2-3 mm long, strigose, the lobes caudate, ca 2-3 mm long; corolla funnelform, white, ca 6-7 mm long, the lobes shallow; stamens 5, the filaments ca 2-2.2 mm long, the anthers ca 0.8-0.9 mm long; ovary ovoid, the style slender, the stigmas clavate. *Fruit* drupaceous, enclosed by the calyx, ellipsoidal, ca 4-5 mm long.

Mexico, Central America, the West Indies, Venezuela, and eastern Brazil.

Fig. 15. *Cordia inermis* (Mill.) I. M. Johnston: A, habit (× 5/7); B, inflorescence (ca × 3). After *Woodson et al. 1478* (GH).

PANAMA: Punta Paitilla, *Standley 26268* (GH).

Johnston (Jour. Arnold Arb. **30:** 98, 1949) described *C. globosa* as comprising two geographic varieties. The typical variety was limited to the Lesser Antilles, Venezuela, and Brazil (with larger, more pointed, and sharply serrate leaves and larger flower-heads), and var. *humilis* to Florida, Mexico, Central America, and the Greater Antilles.

The collection cited above is in fruit only. The floral description was taken from a Mexican specimen [*Hinton 13209* (MO)] which Johnston (loc. cit.) cited.

16. **Cordia spinescens** L., Mant. 2, 206, 1771.

Varronia ferruginea Lam., Tab. Encyc. **1:** 418, 1791.
Cordia ferruginea (Lam.) Roem. & Schult., Syst. Veg. **4:** 458, 1819.

Shrubs or trees, to 5 m. *Leaves* alternate, ovate to ovate-elliptic, coarsely dentate to rarely ± entire, acute to acuminate, the bases rounded to slightly obtuse, to 17 cm long and 9 cm wide, sparsely strigose above and softly-pubescent beneath, sometimes densely so; petioles ca 1-2.5 cm long. *Inflorescences* spikes, scorpioid, to 21 cm long, axillary, the peduncles decurrent with the leaf petioles. *Flowers* perfect, sessile; calyx cupular, ca 2-3 mm long, strigose, 5-toothed, faintly 10-lined or -ribbed; corolla tubular, white to yellow, ca 3-4 mm long, weakly 5-lobed, fimbriolate near the throat; stamens 5, borne on the corolla throat, the filaments ca 1 mm long, the anthers ca 0.6-0.7 mm long; ovary globose, the style slender, ca 3 mm long, twice forked, the stigmas 4. *Fruit* drupaceous, red, ca 3-5 mm long, ovoid; seeds 1-4.

Mexico, Central America, Colombia, and southward along the Andes to Bolivia.

BOCAS DEL TORO: Changuinola to 5 mi S at junction of Ríos Changuinola & Terebe, *Lewis et al. 845* (MO); Water Valley, *von Wedel 1633* (MO), *1672* (MO), *1801* (MO); Chiriquí Lagoon, Old Bank I, *von Wedel 2169* (MO); vic Chiriquí Lagoon, Quebra Nigua, *von Wedel 2741* (MO), Colón I, *von Wedel 2839* (MO). CANAL ZONE: Frijoles, *Ebinger 307* (MO); Corozal, *Greenman & Greenman 5207* (MO); Sabanas, *Riley 117* (MO); Barro Colorado I, nr F. Miller #22, *Shattuck 480* (MO), Gross Trail #8, *Shattuck 1073* (F, MO); Miraflores Locks area, *Tyson 1134* (MO); nr Ft San Lorenzo, *Tyson & Blum 3676* (MO); N side of Canal beyond bridge, *P. White 91* (F, MO); vic Miraflores Lake, *P. White 166* (MO), *245* (MO). CHIRIQUI: Boquete, W slopes of Cerro Horqueta, *Allen 4781* (MO), Finca Collins, *Blum & Duver 2525A* (MO), *Ebinger 705* (MO); Chiquero, *Davidson 557* (F, MO); Cerro Horqueta, *Duke et al. 13628* (MO), *Duver & Hayden 7692* (MO), *Duver et al. 537* (MO); Palto Alto, I of Boquete, *Stern et al. 1088* (MO); Finca Lerida to Pena Blanca, *Woodson & Schery 314* (MO); vic of Bajo Chorro, *Woodson & Schery 613* (MO); Volcan de Chiriqui vic of Casita Alta, *Woodson et al. 912* (MO). COCLE: El Valle de Antón, trails nr Finca Tomás Arias, *Allen 4232* (F, MO). DARIEN: Río Balsa, betw N Quebrada Chusomocatre & Río Areti, *Duke 8706* (MO); Isla Casaya, *Duke 10385* (MO). PANAMA: vic of junction of Río Pacora & Río Corso, *Duke 12009* (MO); thickets & forest nr Arraiján, *Woodson et al. 1357* (MO). SAN BLAS: Veraguas, hills W of Sona, *Allen 1044* (MO); Mulatuppu (Río Ibedi), *Duke 8479* (MO); Sasardi, *Duke 10144* (MO); mainland opposite Ailigandí, from mouth of Río Ailigandí to 2.5 mi inland, *Lewis et al. 165* (MO).

17. **Cordia curassavica** (Jacq.) Roem. & Schult., Syst. Veg. **4:** 460, 1819.

Varronia curassavica Jacq., Enum. 14, 1760.
V. macrostachya Jacq., loc. cit.
Cordia macrostachia (Jacq.) Roem. & Schult., Syst. Veg. 4: 461, 1819.
C. chepensis Pittier, Contr. U.S. Nat. Herb. **18:** 253, 1917.

Shrubs or small trees, to 3 m. *Leaves* alternate, lanceolate-elliptic to ovate-elliptic, coarsely to finely dentate or subentire, acute, the bases obtuse or sometimes attenuate, to 13 cm long and 5 cm wide, sometimes ± coriaceous, the upper surface with small incrustations, each usually bearing a hair, the lower surface softly and densely pubescent; subsessile to petioles ca 5-6 mm long. *Inflorescences* spikes, scorpioid, to 13 cm long, terminal. *Flowers* perfect, sessile; calyx cupular, ca 2.5-3 mm long, 5-toothed, softly-pubescent and covered with resinous dots when young; corolla tubular, white, ca 3.5-4.5 mm long, weakly 5-lobed; stamens 5, borne on the corolla throat, the filaments ca 1.6-1.8 mm long, fimbriolate near the base, the anthers < 1 mm long; ovary ovoid, the style slender, ca 2 mm long, twice divided near the apex, the stigmas 4. *Fruit* drupaceous, ovoid, ca 4-6 mm long and 3.5-5 mm wide, pink to red; seed 1, the cotyledons wrinkled and folded.

Mexico, Central America, the West Indies, and northern South America.

BOCAS DEL TORO: Chiriquí Lagoon, Colón I, *von Wedel 2923* (MO). CANAL ZONE: nr beach at Ft Kobbe, *Duke 4196* (MO); Toro Point nr Ft Sherman, *McDaniel 4996* (MO). COCLE: 10 km W of Agua Dulce on Interamerican Hwy, *Correa 87* (MO); El Valle de Antón, *Seibert 439* (MO); betw Aguadulce and Antón, *Woodson et al. 1207* (MO); betw Las Margaritas & El Valle, *Woodson et al. 1293* (MO). COLON: Nuevo Chagres, beach and adj rdside, *Lewis et al. 1856* (MO). HERRERA: betw Las Minas & Pesé, *Duke 12318* (MO); 12.5 mi S of Ocú, *Lewis et al. 1633* (MO). LOS SANTOS: 1-2 mi W of Candelaria, *Duke 12435* (MO). PANAMA: nr beach at Nueva Gorgona, *Duke 4514* (MO); Cerro Campana, *Duke 10721* (MO). SAN BLAS: Soskatupu, *Duke 10191* (MO). VERAGUAS: 5 mi N Santiago, vic of Río Santa Maria, *Blum & Tyson 624* (MO); 2-4 mi E of Santiago, *Duke 12366* (MO); 2 mi W of Santiago on Transisthmian Hwy, *Dwyer et al. 7550* (MO).

Because of insufficient material, a few collections of *Cordia* remain unnamed:

(1) *Cooper 429* (F, GH) (Bocas del Toro: Daytonia Farm) and *Cooper & Slater 307* (F, US) (Chiriquí: Progreso): trees 6-20 m; leaves obovate, glabrous above, brown-pubescent beneath; fruits yellow to reddish-yellow. These may be referable to *C. collococca* L., which is conspicuously absent from Panama, but a note by Johnston on the *Cooper 429* (GH) sheet refers both collections to *C. invenusta*, an undescribed species. I have not been able to find a valid publication of the above and do not wish to describe a new species from fruiting material alone.

(2) *Lewis et al. 1806* (MO) (Coclé: hills NE of El Valle de Antón): tree to 10 m; leaves ovate-elliptic, sparsely pubescent to ± glabrous on both surfaces; calyx 3-5-lobed; fruits immature. This may be referable to *C. eriostigma* Pittier, but the absence of flowers and the damaged leaves make positive identification difficult.

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

Boraginaceae 33†
Bourreria **48**
  oxyphylla **49**
  panamensis **49**
  superba var. glabra 49
Cerdona alliodora 55
Cordia 33†, **52,** 55†, 56†, 58†, 60†, 68†
  alba 58†
  alliodora **55**
  bicolor **58**
  bifurcata **61**
  cana 65
  chepensis 68
  collococca 68†
  curassavica **68**
  dentata **56**
  diversifolia **53**
  dwyeri **56,** 56†
  eriostigma 68†
  ferruginea 67
  globosa **65,** 67†
  —var. humilis 67†
  inermis **65**
  invenusta 68†
  johnstonii 53
  lasiocalyx **59,** 60†
  lineata **62**
  lucidula 60†, **60**
  macrophylla 55†
  macrostachia 68
  nitida 60†
  panamensis **54,** 55†
  petensis 53
  porcata **61**
  protracta 60†, **60**
  sebestena **58**
  spinescens **67**
  stellifera 55†
  sulcata 55†
  trichostyla 58
Cynoglossum **34**
  mexicanum 35
  officinale **34**
Ehretia **50**
  austin-smithii **51**
Hackelia **35**
  costaricensis 35
  mexicana **35**
Heliophytum
  indicum 37
Heliotropium **37**
  curassavicum **38**
  indicum **37**
  inundatum 38
  lagoense 37†
  procumbens **38**
Lantana inerma 65
Lappula costaricensis 35
Tournefortia **38,** 48†
  angustiflora **43**
  bicolor **45**
  billbergiana 43
  cuspidata **45**
  glabra **43**
  hirsutissima **46**
  johnstonii **48,** 48†
  laevigata 45
  maculata 40†, **40**
  obscura 45
  peruviana 40
  ramonensis 48†
  syringaefolia 40
  volubilis **40,** 40†
Varronia 33†
  curassavica 68
  ferruginea 67
  globosa 65
  lineata 62
  macrostachya 68

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 169. LABIATAE[1,2]

BY JOAN W. NOWICKE AND CARL C. EPLING[3]
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Los Angeles, California

Herbs, annual or perennial, half-shrubs, or shrubs, rarely lianas or trees, usually with aromatic oils, the stems and branches quadrangular, glabrous or pubescent, the hairs frequently uniseriate or glandular. *Leaves* opposite or sometimes whorled, simple or rarely compound, petiolate or sessile, estipulate, the blade usually pinnately-nerved, entire to frequently dentate, glabrous to pubescent, sometimes with resinous[4] dots. *Inflorescences* usually cymes, 2-∞ flowered, sometimes reduced to a single flower,[5] frequently sessile, each cyme then termed a verticillaster, generally opposite, each pair of verticillasters then forming a verticil, arranged as a spike-like raceme, or the verticils congested and forming a head or capitulum, each verticillaster, capitulum, or flower subtended by a bract(s), persistent or deciduous. *Flowers* generally perfect, zygomorphic or rarely actinomorphic; bracteolate or not; sessile to pedicellate; sepals (4-)5, united, bilabiate or regular, persistent, 5-, 10-, 13-, or 15-ribbed; petals 5, sometimes appearing as 4 through reduction or fusion, united, typically bilabiate, the tube straight, arcuate or more sharply bent; stamens 4 and paired, or 2, staminodes rarely present, epipetalous, included or exserted, distinct or rarely monadelphous, the filaments straight or with a variously developed connective, the anthers with 2 functional thecae or sometimes one, dehiscing longitudinally, the thecae parallel or divergent; ovary superior, syncarpous, 2-carpellate, 4-lobed, 2-locular or seemingly 4-locular by a secondary division, placentation basal, gynobase usually present, variously developed as a disc, gynophore, or nectary, the style 1, completely gynobasic or terminal, bifid near the tip, the branches frequently unequal,

[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2] This paper is based on an extensive revision of a manuscript submitted by Epling in December, 1960 - January, 1961. Almost all reductions to synonomy are those found in the original manuscript, and may in some cases be appearing for the first time. Also, as the plates date from 1961 some have no collection cited, and it was impossible to determine the specimens from which they were drawn.

[3] Deceased, November, 1968.

[4] "resinous" is used here in a very general sense, and designates a yellow-green exudate.

[5] Most of the Labiatae have verticillate inflorescences, and it is my opinion that the solitary flower may well represent the ultimate in reduction of the sessile cyme, i.e., only the central flower remains. I have, therefore, described all the inflorescences as being variations of a cyme.

the stigmas minute at the tips. *Fruit* a collection of 4 nutlets, very rarely fleshy, attached at the base or laterally to a columnar extension of the gynobase; seed 1, the testa thin, the endosperm absent or scanty. $x = 6\text{-}11, 13, 17\text{-}20$.

A large family of about 200 genera and 3200 species, cosmopolitan, but with a center of distribution in the Mediterranean region.

About 10 genera are found in Panama, but only *Salvia* and *Hyptis* are represented in any diversity.

Useful references:

Epling, C. C. Synopsis of the South American *Labiatae*. Repert. Spec. Nov. Beih. **85**(1): 1-96, 1935; **85**(2): 97-192, 1936; **85**(3): 193-288, 1936; **85**(4): 289-341, 1937.

KEY TO GENERA

a. Stamens 2.
  b. Only one fertile theca in each anther, calyx bilabiate ..... 1. *Salvia*
  bb. Both thecae fertile in each anther; calyx ± regular with 5 equal teeth ... 2. *Cunila*
aa. Stamens 4.
  c. Stamen filaments united into a short tube above the attachment to the corolla; leaves frequently variegated; corolla tube reflexed near base ..... 3. *Coleus*
  cc. Stamen filaments free; leaves not variegated; corolla tube not sharply reflexed.
    d. Middle lobe of lower corolla lip clearly dipper-shaped; calyx ± regular.
      e. Mature nutlets attached at the base; calyx mostly tubular with vertical veination ..... 4. *Hyptis*
      ee. Mature nutlets attached laterally to a columnar extension of the gynobase; calyx campanulate and with horizontal veins connecting the vertical ..... 5. *Marsypianthes*
    dd. Middle lobe of lower corolla lip plane and spreading; calyx weakly or conspicuously zygomorphic.
      f. Lips of the calyx entire, the upper bearing an erect protuberance flattened contrary to the floral axis ..... 6. *Scutellaria*
      ff. Lips of the calyx variously toothed and without lateral projection of the upper lip.
        g. Calyx conspicuously bilabiate, the upper lip with margins partially or completely decurrent on the tube ..... 7. *Ocimum*
        gg. Calyx weakly bilabiate, the upper lip lacking decurrent margins.
          h. Verticillasters reduced to 1-flower; calyx becoming saccate at maturity ..... 8. *Teucrium*
          hh. Verticillasters ca 3-flowered; calyx enlarging at maturity but not becoming saccate.
            i. Leaves elongate-deltoid, the upper surfaces rugose-areolate ..... 9. *Lepechinia*
            ii. Leaves ovate, the upper surfaces flat ..... 10. *Stachys*

1. SALVIA

Salvia L., Sp. Pl. 23, 1753.

Herbs, annual or perennial, half-shrubs or shrubs, glabrous to pubescent. *Leaves* simple or rarely pinnately compound, opposite, petiolate, pinnately-nerved, entire or generally dentate, glabrous or pubescent, the hairs frequently uniseriate. *Inflorescences* verticils, each with 4 or more flowers, or rarely the flowers solitary and opposite, the bracts deciduous or persistent, sometimes showy. *Flowers* subsessile to shortly pedicellate, the bracteoles generally not apparent; calyx tubular or campanulate, bilabiate, rarely the teeth subequal, the upper lip generally entire or sometimes 3-lobed, 3- or 5-9-veined, the lower lip 2-lobed and generally 6-10-veined, sometimes with glandular capitate hairs; corolla tubular, zygomorphic,

of 5 united petals, blue, white, or red, naked within or with 2-4 papillae or a ring of hairs above the ovary, bilabiate, the upper lip generally entire and plane, the lower 3-lobed; stamens 2, staminodia sometimes present, mounted on the corolla throat, included in the upper lip or exserted, the filaments distinct, the connective elongate, the lower portion straight, retrorsely toothed or geniculate, the anthers generally with one functional theca; ovary 4-lobed, provided with a distinct gynobase generally forming a nectarium, the style arising from the gynobase, long and slender, bifid near the tip, the branches ± equal, or the posterior branch longer. *Nutlets* (1-)4, attached at the base, oblong-ovate, brown.

Salvia is a large genus of 500-900 species with an almost cosmopolitain distribution, being well represented in the tropics, the subtropics of the Mediterranean region and Mexico, and temperate areas. The genus is easily distinguished from the remaining *Labiatae* found in Panama by its stamen number, the presence of only one functional theca in each anther, and the distinct connective.

Ten species of *Salvia* are described from Panama. In the original manuscript of Epling, *S. tiliaefolia* Vahl was treated also, being represented by a single collection, *Allen 217*. However, after comparing the above specimen with non-Panamanian material of *S. tiliaefolia* (all determined by Epling) as well as a photo (MO) of the type [*Berllardi s.n.* (C)], I have concluded that *Allen 217* is a depauperate specimen of *S. longimarginata* Briq. and that *S. tiliaefolia* is absent from Panama or at least as of this date has not been collected there.

a. Corolla generally blue, sometimes rose or white, the tube 2.5-15 mm long; the bracts inconspicuous; the calyx green, or rarely red.
  b. At least some upper calyx lips 5-9-veined, styles glabrous or lightly pubescent.
    c. Corolla tube 2.5-6 mm long, naked within; styles glabrous.
      d. Verticils 6-10-flowered, the bracts ± lanceolate, ca 2-3 mm long and to ca 2 mm wide.
        e. Mature calyces to 4 mm long; stamen connective geniculate below the middle and bearing an assurgent arm ..... 1. *S. occidentalis*
        ee. Mature calyces ca 6 mm long; stamen connective straight, bearing a retrorse tooth near the middle ..... 2. *S. micrantha*
      dd. Inflorescences densely-flowered, globose in appearance, the bracts broadly reniform, ca 10 mm wide ..... 3. *S. hyptoides*
    cc. Corolla tube ca 7-10 mm long, bearing 2-4 well-defined papillae within above ovary; style pubescent near the tip ..... 4. *S. pteroura*
  bb. Upper calyx lip 3-veined; styles pubescent.
    f. Corolla tube bearing 4 papillae within above the ovary.
      g. Corolla tube ca 11-15 mm long; verticils ca 0.5-2 cm distant; at least some pedicels ca 4-6 mm long..... 5. *S. membranacea*
      gg. Corolla tube ca 6-7 mm long; verticils crowded; pedicels ca 0.5-2.5 mm long ..... 6. *S. polystachya*
    ff. Corolla tube naked within.
      h. Leaf blades conspicuously attenuate along the petiole; bracts ca < 3 mm long and tending to be persistent; corolla ca 5-6 mm long ..... 7. *S. longimarginata*
      hh. Leaf blades not conspicuously attenuate; bracts > 4 mm long, mostly deciduous; corolla > 10 mm long.
        i. Delicate herbs; leaves small, ca 2-3 cm long, the bases mostly rounded-truncate, the petioles slender ..... 8. *S. trichopes*
        ii. Coarse herbs; leaves larger, at least some 6 cm long, the bases obtuse ..... 9. *S. alvajaca*
aa. Corolla crimson, the tube 18-34 mm long; the bracts showy; calyx crimson ..... 10. *S. wagneriana*

1. **Salvia occidentalis** Swartz, Prodr. 14, 1788.

Herbs, annuals, prostrate, the branches ca 30-40 cm long, finely pubescent with small ± curved hairs, or glabrous. *Leaves* ovate to ± deltoid, acute, crenate-serrate along the distal margins, the bases obtuse, some truncate or rarely attenuate, to 6 cm long and 3 cm wide, glabrous, or the lower surface pubescent with short hairs; subsessile to petioles ca 1 cm long on lower leaves. *Inflorescences* verticils, 6-10-flowered, pubescent with glandular-capitate hairs, the bracts broadly ovate and long-acuminate, or rhomboid, ca 2-3 mm long, pubescent. *Flowers* with pedicels ca 1-2.5 cm long; calyx tubular, ca 2-4 mm long at maturity, with glandular-capitate hairs, bilabiate, the upper lip mostly 5-9-veined; corolla tubular, ca 2.5 mm long, blue with white streaks, naked within, the upper lip ca 1.2-1.8 mm long, the lower lip weakly 3-lobed, ca 1.5-2 mm long; stamens mounted on the corolla throat, the anthers slender, ca 1 mm long; style slender, the stigma 2-lobed, the lobes flattened. *Nutlets* smooth, ca 1.5 mm long, usually only 1 maturing.

A weedy species of the American tropics.

HERRERA: Ocú, 100 m, *Allen 4089* (MO); vic of Ocú, *Stern et al. 1705* (MO). LOS SANTOS: rd betw Macaracas & Chitre Hwy, *Duver 3155* (MO); rd betw Tonosi & Macaracas, *Oliver et al. 3533* (MO). PANAMA: Taboga I, *Allen 131* (MO), 1-350 m, *Allen 1284* (MO); hills betw Copira & Potrero, 80-130 m, *Dodge & Hunter 8611* (MO), 8629 (MO); forest along telephone trail but as a "weed" on trail betw Rió Indio Hydrographic Sta. & Natural Bridge of Rio Puente, *Dodge & Allen 17480* (MO); Vera Cruz beaches, *Lewis et al. 3017* (MO).

2. **Salvia micrantha** Vahl, Enum. **1:** 235, 1805.

S. orbicularis Benth., Bot Voy. Sulphur 151, 1884.

Herbs, annuals, the stems with appressed hairs, to 40 cm. *Leaves* ± deltoid, acute, crenate, the bases ± truncate or slightly cordate, to 3 cm long and 2 cm wide, ± glabrous above and sparsely pubescent on the veins beneath; petioles to 8 mm long. *Inflorescences* verticils, ca 6-flowered, the bracts lanceolate, ca 2 mm long, early deciduous. *Flowers* pedicellate, ca 2-4 mm long; bracteoles single, narrowly-lanceolate, ca 1-1.5 mm long; calyx tubular, 5-6 mm long at maturity, pubescent with glandular capitate hairs, the upper lobe 2-toothed and mostly 5-9-veined, the lower 3-toothed; corolla tubular, ca 4-5 mm long, blue, naked within, the lower lip much larger; stamens 2, the connective straight or with a slight hook at the tip; style long and slender, bifid at the tip, one branch much longer. *Nutlets* (3-)4, oblong, ca 2 mm long, pale brown.

Widely distributed in Florida and the West Indies; known in Panama only from Manzanillo Island.

PANAMA: Manzanillo I, *Hayes 716* (NY).

This species differs from *S. occidentalis,* to which it is undoubtedly closely related, by its more robust appearance, the structure of its stamen connective, and its slender and unequal stigma lobes.

3. **Salvia hyptoides** Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles **11**(2): 74, 1844.—Fig. 1.

Herbs, annual, erect to 60 cm. *Leaves* deltoid-ovate, acuminate, serrate, the bases truncate to slightly obtuse, to 5 cm long and 3.5 cm wide, both surfaces sparingly pubescent, more so on the veins beneath; petioles ca 1-2 cm long. *Inflorescences* verticils, densely-flowered, globose, 12-15 mm broad, the verticils

Fig. 1. *Salvia hyptoides* Mart. & Gal.: A, habit (ca × ½); B, flower (ca × 8); C, stamens (× 10); D, nutlets (ca × 10). Specimen unknown.

distant below and crowded above, the bracts reniform and acuminate, often membranous, reticulately veined, ca 8-10 mm wide. *Flowers* ± sessile or with pedicels to 1.5 mm long; calyx ± tubular, 3.5-4 mm long, the upper lip with single tooth and ca 5-9-veined, the lower with 2 teeth, pubescent near the apex; corolla tubular, 2.5-3.5 mm long, blue, naked within, the upper lip ca 1 mm long and with glandular-capitate hairs, the lower lip ca 1.5 mm long and spreading; stamens mounted on the corolla throat, the connective retrorsely toothed below the middle, the anthers ca 0.3-0.4 mm long; style glabrous, the stigma with 2 branches acute and rounded. *Nutlets* 3-4, ovate and ± flattened, ca 0.5-0.7 mm long, the testa smooth and pale brown.

Central America, Colombia, and Venezuela.

CANAL ZONE: around El Paraiso, *Pittier 2575* (F). CHIRIQUI: upper valley of Río Chiriquí Viejo, *White & White 105* (MO). DARIEN: Boca de Cupe, 40 m, *Allen 904* (MO). HERRERA: Ocú, 100 m, *Allen 4045* (MO). LOS SANTOS: rd betw Tonosí & Macaracas, *Oliver et al. 3564* (MO). PANAMA: Sabanas nr Chepo, 30 m, *Hunter & Allen* 23 (F, MO). SAN BLAS: vic of Mulatuppu, *Duke 8488* (MO).

4. **Salvia pteroura** Briq., Ann. Conserv. Jard. Bot. Genève, **2:** 139, 1898.

Herbs or subshrubs, the branches ± glabrous, to 2 m. *Leaves* ovate to elliptic, acute, serrulate, the bases obtuse to rounded, sometimes extended along the petiole, to 11 cm long and 5 cm wide, ± glabrous, resin-dotted, petioles ca 1.5-3.5 cm long. *Inflorescences* verticils, 6-12-flowered, arranged in a spike-like raceme, ca 7-10 long, the bracts broadly awl-shaped, ± saccate at the base, long-acuminate, ca 3-5 mm long, deciduous. *Flowers* with pedicels 2-4 mm long; calyx tubular, ca 5.5-8 mm long, membranaceous, sometimes slightly pubescent, the upper lip entire and ± 5-ribbed, the lower lip divided and ca 5-7-ribbed; corolla tubular, 7-10 mm long, blue, with 2-4 papillae near base, the upper lip extended and ca 5-7 mm long, the lower ca 4-5 mm long, pubescent near the distal portion; filaments with a retrorse tooth below the middle, the anthers slender, ca 1.5-1.8 mm long; style long, slender, pubescent near the tip. *Nutlets* 2-4, ovoid, ca 1.5 long, pale brown.

Costa Rica and Panama.

CHIRIQUI: Cerro Vaca, *Pittier 5312* (F). COCLE: vic of El Valle de Antón, *Allen 93* (MO), 600 m, *2764* (MO), *White & White 68* (MO); La Pintada, 400-600 m, *Hunter & Allen 537* (MO).

5. **Salvia membranacea** Benth., Lab. Gen. et Sp. 259, 1833.

S. membranacea var. *villosula* Benth., loc. cit. 720, 1835.
S. compacta var. *irazuensis* O. Ktze., Rev. Gen. Pl. **2:** 530, 1891.
S. irazuensis Fern., Proc. Amer. Acad. **35:** 540, 1900.

Herbs, somewhat suffrutescent, the upper stems and branches with pale brown uniseriate hairs, erect to 2 m. *Leaves* ovate, acute, crenate-serrate, the bases rounded, to 10 cm long and 5 cm wide, sparsely pubescent on both surfaces more so on the veins, petioles to 7 cm long. *Inflorescences* verticils, 8-12-flowered, 5-25 mm distant, the bracts rounded, caducous. *Flowers* with pedicels 2-6 mm long, the bracteole single, inconspicuous, caducous, ca 0.3-0.5 mm long; calyx tubular, ca 5-7 mm long, the upper lip entire and 3-veined, the

lower lip 2-toothed and 5-7-veined, slightly resin-dotted; corolla tubular, ca 15-20 mm long, rose-purple, with 4 papillae above the ovary, the lips ca equal in length, ca 4-5 mm long, the lower more spreading, pubescent at the tip; connectives straight, the anthers ca 1.5 mm long; style long and slender, bifid and pubescent near the tip, the branches unequal. *Nutlets* unknown.

Mexico and Central America.

CHIRIQUI: trail from Cerro Punta to headwaters of Río Caldera, *Allen 1442* (GH, NY); Bajo Chorro, *Davidson 81* (F, MO); Volcán de Chiriquí, *Davidson 926* (A, F), *Woodson et al. 1037* (GH).

6. **Salvia polystachya** Ort., Hort. Matrit. Dec. 55, 1797

S. compacta O. Ktze., Rev. Gen. Pl. **2**: 530, 1891.

Herbs, perennial, stems and branches with appressed hairs, rarely glabrous, to 3 m. *Leaves* ovate, acute-acuminate, serrulate, the bases ± rounded, to 6 cm long and 4.5 cm wide, sparsely pubescent on both surfaces, more so on the veins beneath; petioles ca 1-3 cm long. *Inflorescences* verticils, closely appressed to one another, 12-18-flowered, the bracts ovate and long-acuminate, ca 3 mm long, early caducous. *Flowers* with pedicels 0.5-2 mm long; bracteoles not apparent; calyx tubular, ca 4 mm long, pubescent with uniseriate hairs, resin-dotted, the upper lip entire and 3-veined, the lower 2-toothed and 6-7 veined; corolla tubular, ca 6-7 mm long, blue-violet, with 4 papillae above the ovary, the upper lip ca 4 mm long and pubescent near the tip, the lower lip ca 3 mm long; connectives straight and with a small tooth near the point of attachment, the anthers ca 1 mm long; style long and slender, bifid and pubescent near the tip, the branches unequal. *Nutlets* 4, oblong, ca 1.5 mm long, pale brown.

Central America.

CHIRIQUI: llanos on slopes of Volcán de Chiriquí, *Allen 988* (MO); upper valley of Río Chiriquí Viejo, *Allen 1590* (GH, MO), *White & White 83* (MO), *White 208* (GH); vic of Boquete, *Lewis et al. 396* (MO).

This species is sometimes difficult to separate from *S. membranacea.* The compactness of the verticils in *S. polystachya* is the most distinct difference between them.

7. **Salvia longimarginata** Briq., Ann. Conserv. Jard. Bot. Genève **2:** 127, 1898.

Herbs, perennial, somewhat suffrutescent at the base, to 1-2 m. *Leaves* obovate to rhombate, acute-acuminate, serrate, the bases long-attenuate, to 8 cm long and 5 cm wide, ± glabrous and slightly resin-dotted; petioles indistinct, to ca 5 cm long, winged. *Inflorescences* verticils, each ca 6-flowered, the bracts ca 1.5-2 mm long, ± awl-shaped, seemingly persistent. *Flowers* pedicellate, ca 1.5-3.5 mm long, lightly pubescent; calyx tubular, ca 4-5 mm long, the upper lip entire and 3-veined, the lower lip 2-toothed and ca 7-9-veined; corolla tubular, ca 5-6 mm long, white to blue, naked within, the upper lip ca 1.2-1.3 mm long, the lower lip ca 1.7-1.8 mm long; connectives with a retrorse tooth below the middle, the anthers ca 0.8 mm long; styles long and slender, bifid, the branches conspicuously unequal. *Nutlets* ca 4, oblong-ovate, pale brown, ca 1.5 mm long.

Central America, Colombia, and Venezuela.

CANAL ZONE: forest along telephone trail betw Río Indio Hydrographic Sta & Natural Bridge of Río Puente, *Dodge & Allen 17479* (MO). CHIRIQUI: betw Hato del Jobo & Cerro Voca, *Pittier 5408* (GH); Bismarck, *Williams 255* (NY). COCLE: vic of El Valle, *Allen 217* (GH, MO).

8. **Salvia trichopes** Epling, Bull. Torrey Bot. Club **68:** 564, 1941.

Herbs, or half shrubs, ± glabrous. *Leaves* ovate to ± deltoid, acute, serrate, the bases rounded, ± truncate, or occasionally oblique, to 3.5 cm long and 2 cm wide, glabrous to rarely sparsely pubescent, slightly resin-dotted; petioles slender, ca 1-4 long. *Inflorescences* verticils, each ca 4-6-flowered, the bracts ca 5-6 mm long, long-acuminate and deciduous. *Flowers* with pedicels ca 1-4 mm long, pubescent; calyx tubular, ca 6-7 mm long, bilabiate, the upper lobe entire and 3-veined, the lower lobe 2-toothed and ca 7-veined, sparsely pubescent; corolla tubular, rose, ca 13-15 mm long, naked within, the lips about equal in length, ca 2-2.2 mm long, lightly pubescent near the tip in bud; connectives with a retrorse tooth below the middle, the anthers ca 1 mm long; styles long and slender, bifid, the branches unequal. *Nutlets* ca 4, oblong-ovate, pale brown, ca 1.5 mm long.

CHIRIQUI: vic of Bajo Chorro, *Woodson & Schery* 693 (isotype MO).

Known only from the type collection, the delicate leaves and slender petioles of *S. trichopes,* as well as its corolla length, indicate its distinctness from other *Salvia* species.

9. **Salvia alvajaca** Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 38, 1853.—Fig. 2.

S. ourophylla Briq., Ann. Conserv. Jard. Bot. Genève **2:** 126, 1898.
S. permixta Briq., loc. cit. 129.
S. psilophylla Epling, Bull. Torrey Bot. Club **67:** 527, 1940.

Subshrubs, branches hirtellous, to 2 m. *Leaves* ovate to obovate, acute-acuminate, serrate or weakly serrulate, the bases obtuse, sometimes attenuate or rarely rounded, to 12 cm long and 8 cm wide, sparsely pubescent above and ± glabrous beneath; petioles ca 2-9 cm long. *Inflorescences* verticils, 3-6 flowered, 1-2 cm distant, the bracts awl shaped and keeled at the base, ca 4-6 cm long, deciduous. *Flowers* with pedicels 2-6 mm long; calyx tubular, conspicuously 2-lipped, the lower 2-lobed, the lobes lanceolate, the upper lip entire and 3-veined, the tube ca 4-5 mm long, the lobes ca 3-4 mm long, membranaceous, ca 10-ribbed; corolla tubular, white and tinged with pink or blue, the tube ca 8-10 mm long, naked within, the lips ca equal, ca 3-4 mm long, pubescent near the tips; stamens mounted on the corolla throat, the anthers elongate, ca 1.5-2 mm long; style long and slender, ca 10-12 mm long, bifid, the branches unequal. *Nutlets* (2-)3-4, ovoid, pale brown, ca 1.5 mm long.

Apparently only in Costa Rica and Panama.

CHIRIQUI: Bajo Chorro, *Davidson 60* (paratype of *S. psilophylla,* MO); El Boquete, *Maxon 4964* (F); S slope Volcán de Chiriquí, *Terry 1304* (F); El Volcán, Chiriquí Viejo Valley, *White 99* (GH, MO), *167* (GH); El Volcán, Potrero Muleto to summit, *Woodson & Schery 452* (MO); El Volcán, vic of Callejon Seco, *Woodson & Schery 485* (MO).

Fig. 2. *Salvia alvajaca* Oersted: A, habit (ca × ½); B, flower (ca × 5); C, stamens (ca × 6); D, nutlets (ca × 10). Specimen unknown.

10. **Salvia wagneriana** Polak., Linnaea n.s. **7**: 591, 1877.

S. tonduzii Briq., Ann. Conserv. Jard. Bot. Genève **2**: 157, 1898.—Fig. 3.
S. albopileata Epling in Woodson & Schery, Ann. Missouri Bot. Gard. **27**: 337, 1940.

Herbs, somewhat suffrutescent at the base, perennial, the younger stems with uniseriate hairs, erect to 2 m. *Leaves* ovate, acuminate, serrulate, the bases obtuse

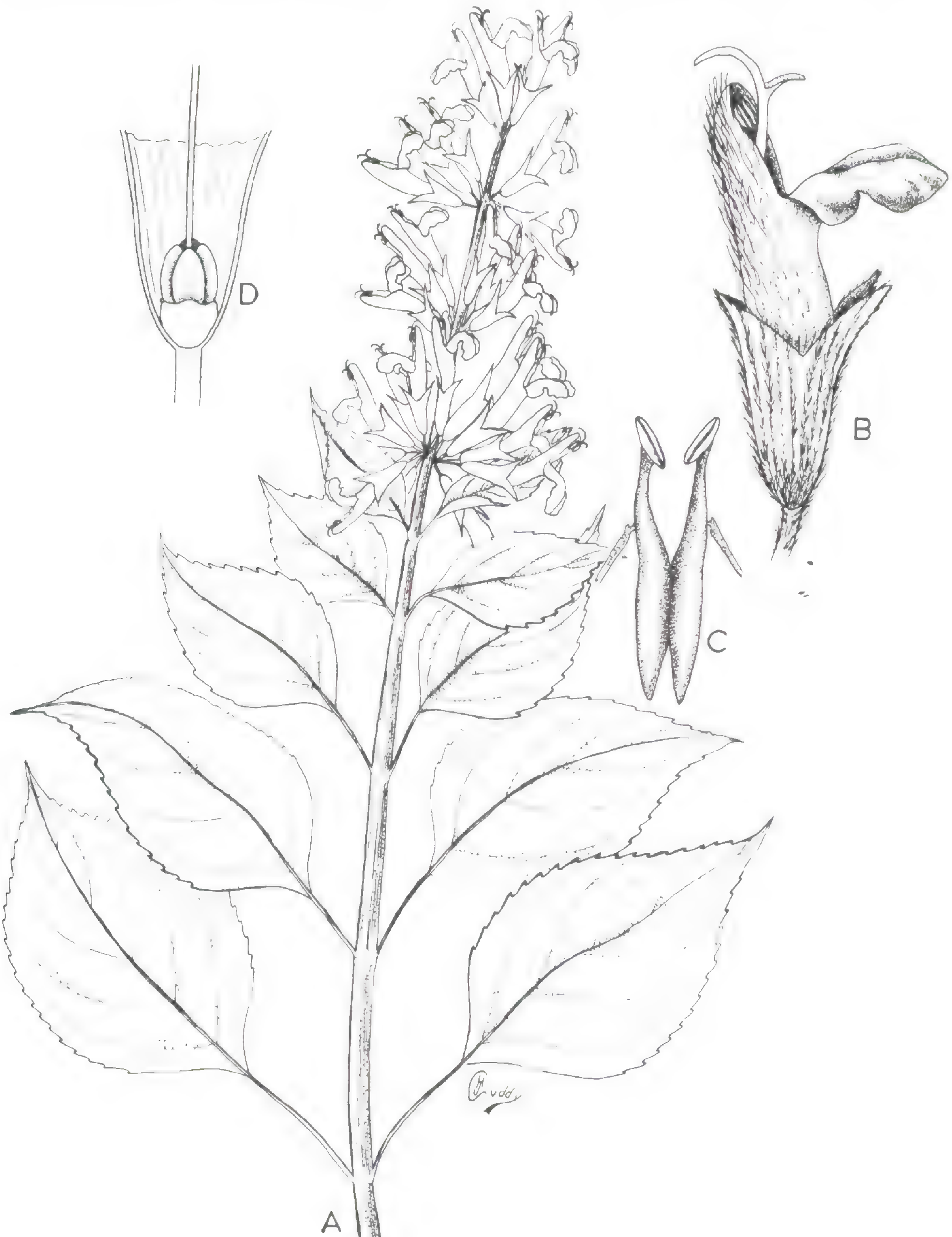

Fig. 3. *Salvia wagneriana* Polak.: A, habit (ca × ½); B, flower (× 2.5); C, stamens (ca × 3.5); D, nutlets (ca × 3). Probably after *White & White 321* (MO).

or rounded, to 13 cm long and 7 cm wide, ± glabrous and resin-dotted; petioles ca 2-5 cm long. *Inflorescences* verticils, paired, ca 1-1.5 cm distant, each with 5-7 flowers, bracts broadly rounded, 6-8 mm long. *Flowers* with pedicels ca 2-10 mm long, covered with uniseriate hairs; bracteoles not apparent; calyx tubular, ca 12-15 mm long, rose, bilabiate, the upper lip entire and ca 7-ribbed, the lower lip 2-toothed and ca 7-ribbed, pubescent with uniseriate and glandular capitate hairs; corolla tubular, ca 18-34 mm long, crimson, with 2 papillae above the ovary, the upper lip ca 3 mm long, the lower lip ca 2 mm long, both pubescent; stamens mounted near the top of the corolla throat, the connective with a long arm, the anthers ca 2-2.2 mm long; styles long and slender, pubescent, the tips bifid, the branches unequal. *Nutlets* (2-)4, oblong, ca 2-2.5 mm long, mottled dark and pale brown.

Apparently only from Costa Rica and Panama.

CHIRIQUI: Volcán de Chiriquí, *Terry 1351* (F, GH); upper Río Chiriquí, *White & White 321* (holotype of *S. albopileata*, MO).

This is perhaps the most showy of the *Salvias* found in Panama.

2. CUNILA

Cunila L., Sp. Pl. ed. 2, 30, 1762.

Half-shrubs or shrubs, scandent or erect. *Leaves* opposite, simple, subsessile to petiolate, pinnately-nerved, generally small. *Inflorescences* verticils and densely-flowered, or loose umbel-like cymes, or capitula and few- to densely-flowered; the bracts generally leaf-like. *Flowers* sessile or pedicellate; bracteoles usually present; calyx tubular, ± actinomorphic or bilabiate, 10-15-veined, pubescent on the inner throat; corolla tubular, white or purple, the tube enclosed or somewhat exserted, bilabiate, sometimes weakly so, the upper lip erect, almost flat, emarginate, the lower lip 3-lobed, the middle lobe widest; stamens 2, exserted, the filaments distinct, the connective not developed, the anthers with 2 functional thecae; ovary 4-lobed, gynobase present, ± cylindrical, the style gynobasic, bifid near the tip, the branches subulate or the anterior somewhat longer and flattened. *Nutlets* (1-)4, attached at the base, ovoid, the pericarp smooth.

A genus of ca 15 species in the New World.

1. **Cunila polyantha** Benth., Lab. Gen. et Sp. 362, 1834.—Fig. 4.

Shrubs, scandent or ± erect, to 1.5 m, softly pubescent on the younger branches or glabrous. *Leaves* ovate to ovate-lanceolate, acute-acuminate, weakly serrulate to subentire, the bases obtuse to ± rounded, to 6 cm long and 3 cm wide, slightly pubescent, more so on the veins beneath; petioles ca 2-5 mm long. *Inflorescences* verticils, rarely cymose, few and crowded, each ca 5-7-flowered, bracts leaf-like, ca 4-5 mm long, deciduous. *Flowers* with pedicels 1-3 mm long; bracteoles present, ± linear, ca 1.5-2 mm long; calyx tubular, ca 3.5-4 mm long, 5-toothed, the teeth deltoid and ± equal, ca 12-15-veined, pubescent, especially on the inner surface of the teeth; corolla tubular, white, exserted, ca 3-4 mm long, weakly bilabiate, the lips ca 1-1.5 mm long, the upper lip cleft, the lower lip 3-lobed, the middle larger, pubescent near the tip; stamens exserted, mounted

Fig. 4. *Cunila polyantha* Benth.: A, habit (ca × ½); B, flower (ca × 10). Probably after *Davidson* 898 (MO).

low in the corolla throat, the anthers small, ca 0.5 mm long; gynobase straight, the style slender, exserted, bifid near the tip, the branches unequal. *Nutlets* ovoid, smooth, mature size unknown.

Mexico and Central America.

CHIRIQUI: Volcán de Chiriquí,*Davidson* 543 (F), 898 (A, MO).

Examination of non-Panamanian collections of *C. polyantha* reveals a noticeable variation in the development of the cymes and their arrangement. In some Mexican material the cymes are numerous, large and conspicuously pedunculate, in contrast to Panamanian specimens where the cymes are few, small and ± sessile, thus forming verticillasters. A photograph (MO) of the type [*Berlandier s.n.* (G)], although admittedly not identical to either of the above mentioned specimens, shows verticils with the more extensive cymose development. In the absence of any comprehensive treatment of the genus, I am not sure of the significance of this variation and hesitate to describe a new species.

3. COLEUS

Coleus Lour., Fl. Cochinch. **2:** 372, 1790.

Herbs, half shrubs, or shrubs. *Leaves* opposite, simple, petiolate, pinnately-nerved. *Inflorescences* verticils, ca 6-flowered, or loose cymes arranged in panicles, racemes, or spikes, the bracts reflexed or deciduous. *Flowers* ± pedicellate; calyx campanulate, bilabiate, the upper lip 3-lobed, the middle lobe largest, the lateral lobes pointed or rounded, the lower lip 2-toothed or -lobed; corolla tubular, reflexed, bilabiate, the upper lip 3-4-lobed, the lower lip boat-shaped or concave and entire; stamens 4, curved into the lower lip, monadelphous, sometimes weakly so, the short tube free from the corolla, the anthers with 2 functional thecae; ovary 4-lobed, the gynobase variously developed, sometimes as a nectary, the style gynobasic, bifid near the tip, the branches equal and acute. *Nutlets* ca 4, attached at the base, ovoid to ovoid-spherical, smooth.

Variously described as having 100-200 species, mostly in warmer regions of the old world.

A single introduced species in Panama.

1. **Coleus blumei** Benth., Lab. Gen. et Sp. 56, 1832.

Herbs, somewhat succulent, sprawling, the stems to 70 cm long, the younger branches pubescent. *Leaves* ovate, ± acute, crenate, the bases truncate, to 4 cm long and 3.5 cm wide, sparsely pubescent above and on the veins beneath, resin-dotted, sometimes variegated; petioles ca 1-4 cm long. *Inflorescences* cymes, loosely-flowered, the lateral branches developed, the bracts deciduous. *Flowers* with pedicels 1-2 mm long; bracteoles not apparent; calyx ca 2 mm long, pubescent, resin-dotted, the upper lip 3-lobed, the middle lobe much larger, the 2 laterals rounded, the lower lip much smaller and 2-toothed; corolla ca 1 cm long, purple, exserted, the tube sharply recurved, the upper lip 2-lobed, the lower lip boat-shaped, entire and becoming enlarged; filaments glabrous, united near their bases, the anthers ca 0.6-0.7 mm long; ovary 4-lobed, the gynobase asymmetrical and becoming enlarged in fruit, the style bifid near the tip, the branches ± equal.

Nutlets 4, somewhat compressed laterally, ca 1 mm in diam, brown.

Native of the East Indies, but widely introduced elsewhere because of its ornamental properties.

COCLE: El Valle de Antón, *Lewis et al. 2514* (MO).

4. HYPTIS

Hyptis Jacq., Coll. **1:** 101, 1787. nom. cons.

Mesosphaerum P. Br., Hist. Jamaic. 257, *pl. 18, f. 3*, 1756.

Herbs, coarse, half-shrubs, shrubs, or rarely trees. *Leaves* opposite, simple, mostly petiolate, pinnately-nerved. *Inflorescences* verticils, arranged as a spike or raceme, or congested into dense capitula, ± sessile or pedunculate; bracts linear to ovate. *Flowers* sessile or pedicellate; bracteoles present or not apparent; calyx tubular or campanulate, ± actinomorphic, rarely bilabiate, often enlarging in fruit, generally membranaceous and ca 10-veined, the tube straight, bent, or curved, the teeth deltoid, linear or spinulose; corolla tubular, white, blue, or rose-purple, glabrous or pubescent, bilabiate, the upper lip 2-lobed, the lower lip usually longer and 3-lobed, the middle lobe saccate; stamens 4, paired, mounted on the corolla throat, curved into the lower lip or exserted over it, the filaments distinct, the connective not developed, the anthers with 2 functional thecae, frequently red to purple, mostly divergent; ovary 4-lobed, gynobase lobed and somewhat elongated, the style gynobasic, long and slender, branched near the tip, the lobes small, clavate and ± equal. *Nutlets* (1-)4, attached at the base, ovoid-cylindrical or ± flattened, sometimes with 2 slight depressions on the lobes of the gynobase adhering, brown.

About 300 species in the warmer regions of the New World, especially Brazil, and a few representatives in the Old World tropics.

Useful reference:

Epling, C. C. Revisión del genero *Hyptis (Labiatae).* Revista Mus. La Plata Bot. **7:** 153-497, 1949.

a. Verticils few-flowered, distant.
  b. Calyx teeth deltoid ..... 1. *H. verticillata*
  bb. Calyx teeth linear or spinulose.
    c. Robust herbs; inflorescences open, peduncles ca 0.5 1 cm long; calyx tubes 5-7 mm long; bracts ± deciduous ..... 2. *H. suaveolens*
    cc. Weak herbs; inflorescences more compacted, sessile, or with peduncles < 0.5 cm long; calyx tubes < 3 mm long; bracts persistent.
      d. Bracteoles linear; inflorescences + scorpioid; conspicuous white tuft of hair between calyx teeth ..... 3. *H. pectinata*
      dd. Bracteoles ovate; inflorescences semiglobose; no conspicuous white tuft of hair between calyx teeth ..... 4. *H. mutabilis*

aa. Verticils congested into dense capitula, or if doubtful, then plant with branched hairs.
  e. Inflorescences sessile or shortly pedunculate; the cleft between the upper calyx teeth cut more deeply ..... 5. *H. pulegioides*
  ee. Inflorescences pedunculate; calyx teeth cut ± evenly.
    f. Outer bracts filiform to linear; calyx tube at maturity recurved above the middle ..... 6. *H. recurvata*
    ff. Outer bracts lanceolate, spatulate, or ovate; calyx tube ± straight at maturity.

g. Stems and under surfaces of leaves with branched hairs . . 7. *H. oblongifolia*
gg. Hairs simple.
h. Leaves definitely sessile, the bases truncate and clasping; inflorescences conspicuously whitish-pubescent . . . . . 8. *H. dilatata*
hh. Leaves petiolate, or if subsessile, then with narrowed bases; inflorescences not conspicuously whitish-pubescent.
i. Calyx tube naked within, sometimes pubescent near orifice but not pilose-annulate above the nutlets.
j. Peduncles <1.2 cm long.
k. Calyx <2 mm long, the teeth deltoid . . . . . 9. *H. obtusiflora*
kk. Calyx > 3 mm long, the teeth spinulose . . . . 10. *H. brevipes*
jj. At least some peduncles 2 cm long or longer.
l. Robust, erect herbs; peduncles stout; at least some leaves > 5 cm long . . . . . 11. *H. brachiata*
ll. Slender, prostrate herbs; peduncles slender; leaves mostly 2.5-3.5 cm long . . . . . 12. *H. atrorubens*
ii. Calyx tube distinctly pilose-annulate within above the nutlets.
m. Calyx tube conspicuously longer than the teeth . . 13. *H. capitata*
mm. Calyx tube and teeth about equal in length.
n. Slender herbs; leaves ± ovate, ca 3-4 long; bracts ovate and crenate . . . . . 14. *H. lantanaefolia*
nn. Robust, coarse herbs; leaves lanceolate, or if rarely ovate-lanceolate then > 5 cm long; bracts ± awl-shaped and entire.
o. Bracts glabrous; mature capitula ± globose . . . . . 15. *H. savannarum*
oo. Bracts with soft pale brown pubescence; mature capitula ± hemispheric . . . . . 16. *H. conferta*

1. **Hyptis verticillata** Jacq., Coll. **1**: 101, 1787.

Mesosphaerum verticillatum (Jacq.) O. Ktze., Rev. Gen. Pl. **2**: 525, 1891.

Herb or half shrub, perennial, 1-3 m tall, the branches appressed-puberulent and generally bearing spreading longer hairs along the angles. *Leaves* elliptical or oblong-lanceolate, acute, serrulate or subentire, the bases obtuse, to 7 cm long and 2 cm wide, both surfaces lightly pubescent and often bearing longer hairs along the principal veins, resin-dotted; petioles ca 5-10 mm long, the upper leaves sometimes subsessile. *Inflorescences* verticils, 12-15-flowered, ± moniliform, arranged in panicles in the axils of the upper reduced leaves; bracts linear, ca 1-2 mm long, setaceous. *Flowers* with pedicels ca 0.5-1 mm long, tufts of hairs at the bases; calyx tubular, ca 2 mm long at maturity, teeth ± lanceolate-deltoid, ca 1 mm long, the tube distended at maturity by the nutlets, the teeth somewhat connivent; corolla ca 2-3 mm long, blue and white, exserted, the lobes ca 1 mm long, ± pubescent; stamens exserted, the filaments lightly pubescent, the anthers ca 0.1-0.2 mm long; gynobase lobed, the style ca 2 mm long. *Nutlets* 2-4, ovoid-oblong, ca 1.5-1.7 mm long, the lobes of the gynobase sometimes adhering, the pericarp somewhat corky.

A widespread weed of the American tropics.

BOCAS DEL TORO: Changuinola to 5 mi S at junct of Ríos Changuinola & Terebe, *Lewis et al. 920* (MO); Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1983* (MO); s. loc., *von Wedel 326* (MO); vic of Chiriquí Lagoon, Cocoa Cay, *von Wedel 2878* (MO). CANAL ZONE: Río Chagres, *Fendler 221* (MO); Ft San Lorenzo, *Tyson 2240* (MO); vic of Miraflores, *G. White 125* (F, MO); s. loc., s. coll. *(MO 1119508)*. DARIEN: Río Balso betw Quebrada Chusomocatre & Río Areti, *Duke 8274* (MO); Tucute, *Terry & Terry 1401* (F, MO). PANAMA: Taboga I, *Allen 1302* (MO); Río Pita, 1-3 above confluence with

Río Maestra, *Duke 4732* (MO); Río Chagres tributary, 5 mi SW Cerro Brewster, *Lewis et al. 3466* (MO); Chepo, *Tyson 1427* (MO); Canita, 18 m E of Chepo, *Tyson & Smith 4138* (MO). SAN BLAS: mainland opposite Achituppu to 1.5 mi inland, *Lewis et al. 96* (MO). PROVINCE UNKNOWN: *Andersson s. n.* (MO).

2. **Hyptis suaveolens** (L.) Poit., Ann. Mus. Hist. Nat. Paris **7:** 472, *pl. 29, f. 2*, 1806.

Ballota suaveolens L., Syst. Nat., ed. 10, 1100, 1759.
Mesosphaerum suaveolens (L.) O. Ktze., Rev. Gen. Pl. **2:** 525, 1891.

Herbs, coarse, slightly suffrutescent at the base, to 3 m, lightly to densely pubescent, the hairs uniseriate and to 3 mm long, some glandular-capitate. *Leaves* deltoid, ovate, or rhombate, acute, serrate to doubly serrate, the bases cordate to rounded, to 8(-12) cm long and 6(-8) cm wide, pubescent on both surfaces, densely so on the veins beneath; petioles to 7 cm long. *Inflorescences* cymes, 3-6-flowered, the peduncles ca 0.5-2 cm long, the bracts leaflike, caducous. *Flowers* subsessile; calyx narrowly campanulate, ca 4.5-6(-8) mm long at maturity, teeth spinulose, ca 2(-3.5) mm long, ca 10-ribbed, membranaceous, pubescent; corolla purple, the tube ca 4-5 mm long, exserted, the lips ca 1.5-2 mm long, pubescent; filaments pubescent, the anthers ca 0.3 mm long; style slender, ca 4 mm long, weakly 2-lobed. *Nutlets* 1(-2), rectangular, ca 3 mm long, the pericarp corky and dark brown.

Widely distributed in the tropics of North and South America, and also found in the East Indies to Hong Kong and Formosa, Australia, and Africa.

BOCAS DEL TORO: Columbus I., 6 mi inland, *von Wedel 34* (MO); vic of Chiriquí Lagoon, Careening Cay, *von Wedel 2818* (MO). CANAL ZONE: sabanas along drowned Río Azote Caballo, *Dodge et al. 16834* (MO). COCLE: vic Río Teta & Pan Am Hwy, *Blum & Tyson 1892* (MO). DARIEN: vic of El Llano, *Duke 5795* (MO). PANAMA: betw Capira & Potrero, *Dodge & Hunter 8640* (MO); 5-6 mi E of Chepo on Pan Am Hwy, *Duke 4049* (MO); nr beach at Nueva Gorgona, *Duke 4490* (MO).

3. **Hyptis pectinata** (L.) Poit., Ann. Mus. Hist. Nat. Paris **7:** 474, *pl. 30*, 1806.

Nepeta pectinata L., Sp. Pl. 799, 1753.
Mesosphaerum pectinatum (L.) O. Ktze., Rev. Gen. Pl. **2:** 525, 1891.

Herbs, perennial, to 3 m, stems pubescent and generally scabrous along the angles. *Leaves* ovate to ± deltoid, acute, double serrate, the bases truncate to slightly obtuse, to 3.5(-8) cm long 2(-4.5) cm wide, pubescent on both surfaces, densely so beneath, sparsely resin-dotted; petioles to 5 cm long on mature leaves. *Inflorescences* cymes, each with 2-3 semi-scorpioid branches, the peduncles ca 1-2 mm long, the bract leaf-like, 3-4 mm long. *Flowers* subsessile; bracteole linear, ca 3-4 mm long, pubescent; calyx tubular, ca 2 mm long at maturity, 10-ribbed, pubescent, the teeth spinulose, ca 1-2 mm long, a conspicuous tuft of white hairs between the teeth; corolla tube ca 1.5 mm long, exserted, rose-purple above, ± cream below, pubescent, small and inconspicuous, the lips ca 0.5-0.6 mm long; stamens ± sessile, the anthers ca 0.1 mm long; gynobase somewhat lobed, style seemingly enclosed. *Nutlets* 3-4, oblong, ca 0.7-0.9 mm long.

A widespread but not abundant weed of the American tropics; to be expected at lower elevations.

DARIEN: Cerro Pirre, *Duke & Elias 13676* (MO). LOS SANTOS: 17.8 mi S of Macaracas, *Lewis et al. 1614* (MO); 25 mi SW of Tonosí, headwaters of Río Pedregal, *Lewis et al. 2963* (MO). PANAMA: Cerro Jefe, *Duke 9389* (MO), *Dwyer et al. 7267* (MO); Isla del Rey, *Duke 9544* (MO).

4. **Hyptis mutabilis** (A. Rich.) Briq., Bull. Herb. Boissier **4:** 788, 1896.

Nepeta mutabilis A. Rich., Actes Soc. Hist. Nat. Paris 110, 1792.
Mesosphaerum mutabile (A. Rich.) O. Ktze., Rev. Gen. Pl. **2:** 525. 1891.

Herbs, to 3.5 m. *Leaves* ovate or rhomboid, acute, serrate to doubly serrate, the bases truncate or obtuse, to 6 cm long and 3.5 cm wide, ± hirsute on the upper surfaces, ± pubescent below, particularly along the veins, subsessile to petioles ca 2-3 cm long. *Inflorescences* verticils, 3-10-flowered, the peduncles ca 0.5-1 cm long at maturity, arranged as a panicle 5-15 cm long, the bracts leaflike. *Flowers* sessile; bracteoles ovate or ovate-lanceolate, ca 4-6 mm long, pubescent and ciliate along the margins; calyx tube ca 1.5-2 mm long, elongating to ca 5-6(-7) mm long at maturity, membranaceous, pubescent, 10-ribbed, the teeth spinulose, ca 1 mm long; corolla tube ca 4-5 mm long, purple to lavender, the lips <1 mm long, pubescent; stamens exserted, the filaments pubescent, the anthers ca 0.2 mm long; style ca 4.5-5.5 mm long. *Nutlets* (2-)3-4, ovoid, ca 2 mm long, dark brown.

A common weed of roadsides and second growth areas, widely distributed in the American tropics.

CANAL ZONE: betw Gorgona & Mamei, *Pittier 2240* (F). CHIRIQUI: vic of Boquete, *Davidson 586* (F, MO); Valley of Río Chiriquí Viejo, N of Volcán City, *Duke 9030* (MO); from Boquete to 3 mi N, *Lewis et al. 345* (MO), *349* (F, MO). COCLE: vic El Valle, *Allen 1179* (MO); El Valle de Antón, nr Finca Tomás Arias, *Allen 4224* (MO); El Valle de Antón, *Lewis et al. 2520* (MO); Río Hata Military Res along Pan Am Hwy, *Tyson & Blum 2556* (MO). DARIEN: Ridge NW of Yaviza, *Duke 6532* (MO); 8 mi N of Santa Fé, Agua Fria, *Duke 10117* (MO); Cerro Piriaque, *Tyson et al. 3822* (MO). HERRERA: vic of Chitré, *Allen 1107* (MO). LOS SANTOS: Punta Mala, *Tyson 2710* (MO).

5. **Hyptis pulegioides** Pohl ex Benth., Lab. Gen. et Sp. 128, 1833.

Mesosphaerum pulegiodes (Pohl ex Benth.) O. Ktze., Rev. Gen. Pl. **2:** 527, 1891.

Herbs, erect to 60 cm, pubescent with uniseriate appressed hairs. *Leaves* elliptic-lanceolate, acute, entire or mostly dentate, to ca 3.8 cm long and ca 1-2.5 cm wide, pubescent on both surfaces, more so on the veins beneath. *Inflorescences* capitula, ca 1 cm wide, axillary, sessile to peduncles ca 1 cm long, the bracts filiform, ca 3-4 mm long. *Flowers* crowded, very pubescent at their bases; calyx tube ca 2-3 mm long, membranaceous, the teeth lanceolate, ca 1 mm long, the cleft between the upper teeth cut more deeply; corolla ca 1-1.5 mm long, the tube naked within, the lips ca 0.2-0.3 mm long, sparingly pubescent; stamens weakly exserted, the anthers 0.1-0.2 mm long; style shortly exserted. *Nutlets* (3-)4, ovate, ca 0.5 mm long, pale brown.

Infrequent in Panama; scattered throughout Central America and northern South America.

CHIRIQUI: Cerro Vaca, in savannas, *Pittier 5343* (F). PANAMA: sabanas nr Chepo, *Hunter & Allen 55* (MO, in part).

6. **Hyptis recurvata** Poit., Ann. Mus. Hist. Nat. Paris **7:** 467, *pl. 28, f. 1,* 1806. -Fig. 5.

Mesosphaerum recurvatum (Poit.) O. Ktze., Rev. Gen. Pl. **2:** 527, 1891.

Herbs, annuals, slender, lightly pubescent, to 1 m. *Leaves* ovate to elliptic, acute, crenate, the bases rounded to ± obtuse, to 3 cm long and 2 cm wide, lightly pubescent on both surfaces; petioles ca 0.3(-4) cm long. *Inflorescences* capitula, ca 1 cm diam, the peduncles slender, ca 1-3 cm long, the bracts filiform to linear, ca 2.5-3 mm long, fimbriolate. *Flowers* subsessile; calyx tubular, ca 3 mm long, becoming saccate at the base and constricted and distinctly recurved above the middle, pubescent near the orifice, the teeth spinulose, ca 1-1.2 mm long; corolla tube ca 2 mm long, white, the lips ca 0.7-1 mm long, sparsely pubescent; stamens exserted, the filaments glabrous, the anthers 0.2 mm long; style exserted, the branches minute. *Nutlets* 4, oblong-ovoid, ca 0.8-1 mm long, pale brown.

Parts of Central America and northern South America.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al.* 2737 (MO). CANAL ZONE: Barro Colorado I, *Croat* 4737 (MO); s. loc., *Eppelsheimer s.n.* (F). CHIRIQUI: llanos W of Gualaca, *Allen* 5045 (MO); 12.4 mi N of David, *Lewis et al.* 720 (MO); vic of San Félix, *Pittier* 5433 (F). PANAMA: Pacora, 35 mi, *Allen 1003* (MO); San José I, disturbed area, *Johnston 1294* (MO); Panama, *Bro. Paul* 527 (MO).

7. **Hyptis oblongifolia** Benth. in DC., Prodr. **12:** 125, 1848.

H. vulcanica Seem., Bot. Voy. Herald, 188, 1854.
Mesosphaerum oblongifolium (Benth.) O. Ktz., Rev. Gen. Pl. **2:** 526, 1891.
M. vulcanicum (Seem.) O. Ktze., loc. cit., 527.

Shrubs, sometimes small trees, to ca 2 m, the branches ± lanate with branched hairs. *Leaves* ovate-elliptic, acute, finely serrate, the bases rounded to obtuse, to 8 cm long and 4 cm wide, pubescent on both surfaces, the hairs generally simple and uniseriate above, branched and extremely dense beneath; petioles ca 1-3 cm long, densely pubescent. *Inflorescences* ± capitulate, axillary, loosely-flowered, ca 0.5-1 cm diam, the peduncles ca 0.5-1 cm long, the capitula sometimes arranged in a cymose pattern, the bracts linear, masked by the dense pubescence. *Flowers* subsessile; calyx campanulate, ca 2.5-3 mm long, naked within, densely pubescent without, obscurely 10-veined, the teeth spinulose, ca 2-3 mm long; corolla tube ca 4-5 mm long, lavender, the lower lip ca 1.5 mm long, both lips pubescent; stamens exserted, the filaments pubescent, the anthers ca 0.4 mm long; style long exserted, ca 4-5 mm long, the lobes rounded, small and equal. *Nutlets* unknown.

Common in Mexico and sparsely distributed in Guatamala, Costa Rica, and Panama.

CHIRIQUI: Boquete, *M. E. Terry 1272* (A, F); *Terry & Terry 1639* (F). PANAMA: swamp E of Río Tucumen, *Standley* 26623 (GH).

Although the branched hairs are unique, the density of the pubescence tends to mask this character.

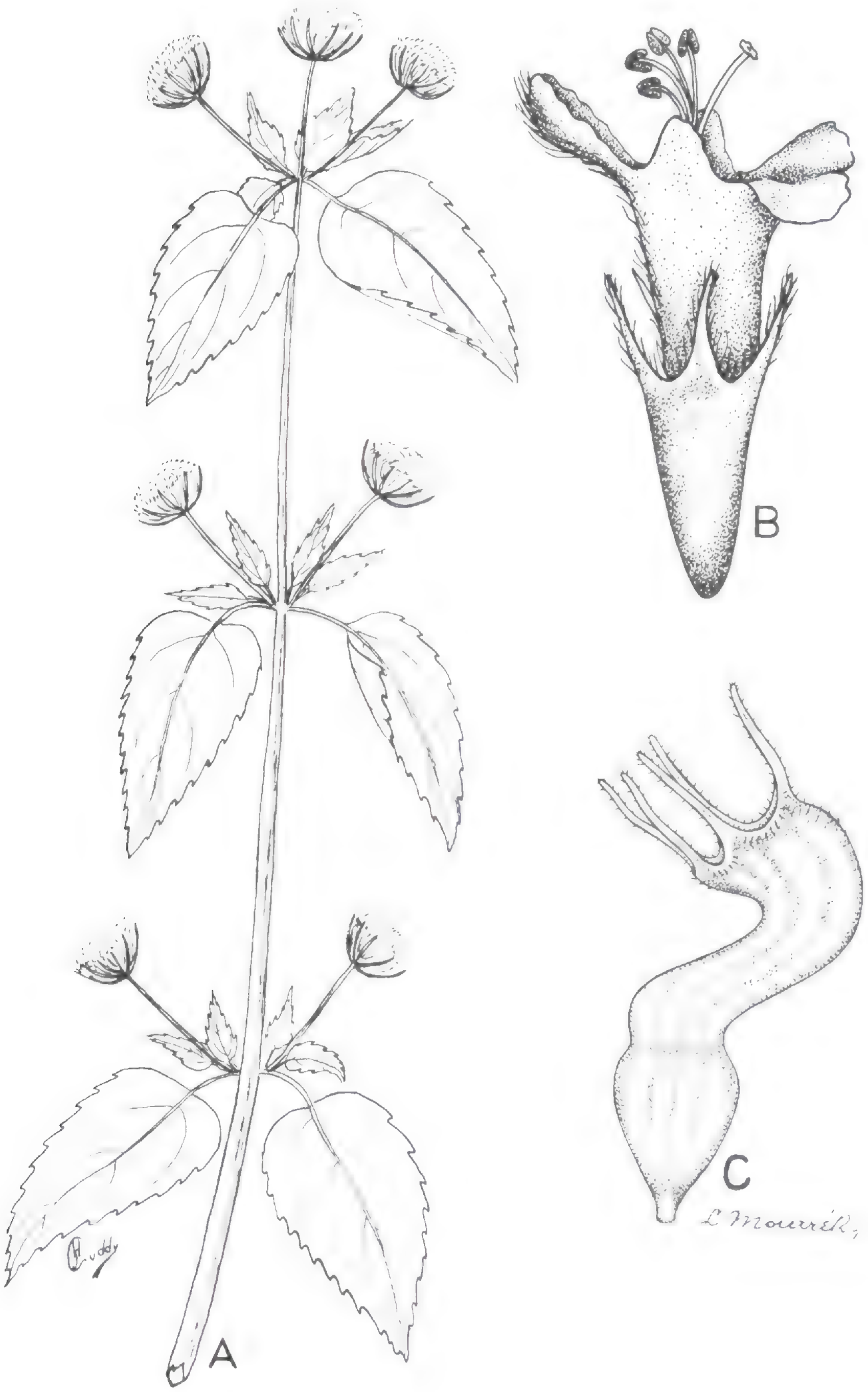

Fig. 5. *Hyptis recurvata* Poit.: A, habit (ca × 1); B, flower (ca × 8); C, mature calyx (ca × 20). A-B, specimen unknown. C, after *Croat* 4737 (MO).

8. **Hyptis dilatata** Benth. in DC., Prodr. **12:** 103, 1848.—Fig. 6.

H. crenata var. *augustifolia* Benth. ex Seem., Bot. Voy. Herald, 187, 1854.
Mesosphaerum dilatatum (Benth.) O. Ktze., Rev. Gen. Pl. **2**: 526, 1891.

Herbs or subshrubs, pubescent with uniseriate and glandular hairs, to ca 1 m. *Leaves* oblong-lanceolate, acute, crenate, the bases truncate, to 5 cm long and 1.5 cm wide, pubescent on both surfaces, densely so beneath; sessile. *Inflorescences* capitula, ca 1-1.5 cm wide, the peduncles 1.5-3.5 cm long, the bracts linear or subulate, ca 7-10 mm long, densely pubescent. *Flowers* sessile, tufts of uniseriate hairs at the base, each 2-3 mm long; calyx ± campanulate, ca 2.5-3

Fig. 6. *Hyptis dilatata* Benth.: A, habit (× ½); B, flower (ca × 8); C, stamens (ca × 10); D, nutlets (ca × 8). After *Allen 1015* (MO).

mm long at maturity, membranaceous, ± 10-ribbed, resin-dotted, the teeth ca 1-1.8 mm long and conspicuously pubescent; corolla tube ca 3-3.5 mm long, blue (?), the lips ca 1 mm long, slightly pubescent; stamens exserted, the filaments ± glabrous, the anthers ca 0.3-4 mm long; style long exserted. *Nutlets* (2-) 4, ovoid, ca 1.5 mm long, pale brown.

Panama and northern South America.

COCLE: betw Paso del Arado & Ola, *Pittier 5015* (F). HERRERA: 5 mi S of Ocú, *Stern et al. 1687* (MO). VERAGUAS: vic of Santiago, *Allen 1015* (MO).

9. **Hyptis obtusiflora** Presl ex Benth., Lab. Gen. et Sp. 107, 1833.—Fig. 7.

Mesosphaerum obtusiflorum (Presl ex Benth.) O. Ktze., Rev. Gen. Pl. **2**: 525, 1891.

Herbs, ± suffrutescent at the base, to 1.5 m. *Leaves* ovate, the upper ± elliptic, acute, serrate, the bases obtuse to attenuate, to 8 cm long and 3.5 cm wide, sparsely pubescent on both surfaces, more so on the veins beneath, resin-dotted; subsessile to petioles 0.5-1 cm long. *Inflorescences* capitula, dense, axillary, sessile to peduncles ca 1 cm long; bracts ovate-lanceolate, ca 3-4 mm long. *Flowers* sessile; calyx short-tubular, ca 1-1.5 mm long, ± naked within, teeth ± deltoid, ca 0.7-1 mm long, saccate at maturity and distended by the nutlets; corolla tube 2-3 mm long, white, slightly pubescent, the lips ca 1 mm long; stamens slightly exserted, the filaments pubescent, the anthers 0.3 mm long; style long exserted. *Nutlets* (3-)4, ovate, ca 0.6-0.7 mm long, dark brown, pubescent at the distal portion.

Costa Rica, Panama, and northwestern South America.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2729* (MO); Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2070* (MO). COCLE: El Valle de Antón, *Lewis et al. 2513* (MO). COLON: along Río Iguanitas, *Elias & Kirkbride 1631* (MO).

10. **Hyptis brevipes** Poit., Ann. Mus. Hist. Nat. Paris **7**: 465, 1806.

Mesosphaerum brevipes O. Ktze., Rev. Gen. Pl. **2**: 525, 1891.

Herbs, annual, erect or sometimes sprawling, to 60 cm, pubescent, the hairs long and uniseriate. *Leaves* lanceolate-elliptic, rarely rhomboid-ovate, acute, doubly or irregularly serrate, the bases attenuate, to 5 cm long and 2 cm wide, pubescent on both surfaces, more so on the veins beneath, resin-dotted; sessile to petioles ca 1 cm long. *Inflorescences* capitula, ca 1 cm in diam, the peduncles ca 0.5-1 cm long, the bracts awl-shaped and ciliate, ca 4-6 mm long. *Flowers* sessile, tufts of hairs at the bases; calyx ± campanulate, 3-3.5 mm long at maturity, lightly pubescent within near the orifice, obscurely 10-nerved, the teeth spinulose, ca 1.5-2 mm long; corolla ca 3 mm long, white, the lower lip ca 0.6-0.8 mm long, pubescent, the hairs uniseriate; stamens weakly exserted, the filaments ± pubescent, the anthers ca 0.2 mm long; styles ca 3 mm long, the lobes small. *Nutlets* 4, oblong-ovoid, ca 0.6 mm long, the pericarps slightly roughened, dark brown.

A widely distributed weed in tropical America, from Mexico to Argentina, but probably native to Brazil (Epling, 1949).

CANAL ZONE: Barro Colorado I, Miller Trail, *Shattuck 479* (F). COLON: along Río Sirri, Trinidad Basin, *Pittier 4023* (F).

Fig. 7. *Hyptis obtusiflora* Presl.: A, habit (× ½); B, flower (ca × 18); C, stamens (ca × 15); D, nutlets (ca × 30). After *Woodson et al. 1906* (location unknown).

11. **Hyptis brachiata** Briq., Ann. Conserv. Jard. Bot. Genève **2:** 215, 1898.

Mesosphaerum brachiatum Briq., loc. cit., pro syn.

Herbs or subshrubs, robust, ± densely soft-pubescent, to 2 m. *Leaves* ovate or sometimes ± elliptic, acute, crenate-serrate, the bases rounded to obtuse, to 8.5 cm long and 4.5 cm wide, pubescent on both surfaces, densely so beneath; petioles ca 0.5-1 cm long. *Inflorescences* capitula, axillary, the peduncles ca 1-2 cm long, pubescent, the bracts mostly ovate, ca 6-9 mm long, pubescent. *Flowers* sessile; calyx tubular, ca 2 mm long, ± naked within, pubescent and resin-dotted, membranaceous, the teeth spinulose, ca 2.5-3 mm long, ciliate between; corolla tube ca 4-5 mm long, the lower lip longer, ca 2 mm long, slightly pubescent and resin-dotted; stamens exserted, the filaments glabrous, the anthers ca 0.2-0.3 mm long. *Nutlets* ca (3-)4, flattened ovoid, 2 depressions near the base, 1.4-1.5 mm long, the pericarp verrucose.

Costa Rica, Panama, Colombia, and Venezuela.

CANAL ZONE: hill opposite Paraíso Development, *Duver 7152* (MO). COCLE: hills S of El Valle de Antón, *Allen 2816* (F). PANAMA: along rd nr top of Cerro Campana, *Duke 5963* (MO).

12. **Hyptis atrorubens** Poit., Ann. Mus. Hist. Nat. Paris **7:** 466 *pl.* 27, *f.* 3, 1806.—Fig. 8.

Mesosphaerum atrorubens (Poit.) O. Ktze., Rev. Gen. Pl. **2:** 525, 1891.

Herbs, slender, prostrate, rooting at the nodes, stems to 3 m long, lightly pubescent. *Leaves* ovate, acute, crenate-serrate, the bases rounded and attenuate, 2.5-3.5 cm long and 1-1.5 cm wide, sparsely pubescent, resin-dotted; petioles ca 0.5-1.5 cm long, narrowly margined. *Inflorescences* capitula, axillary, hemispheric, 8-10 mm in diam, the peduncles ca 0.5-2.5 cm long, the bracts obovate, 4-6 mm long, ciliate. *Flowers* sessile, tufts of hair at the bases; calyx tubular, ca 3.5-4 mm long at maturity, naked within, the teeth acicular to setaceous, ca 1-1.2 mm long, pubescent between; corolla ca 4-5 mm long, white, the lower lip ca 1 mm long, pubescent; stamens shortly exserted, the filaments lightly pubescent, the anthers ca 0.2 mm long; gynobase weakly lobed, the style ca 4-5 mm long, minutely bifid near the tip. *Nutlets* 4, ovoid-oblong, ca 0.6-0.8 mm long, the pericarp verrucose.

Mexico, Guatemala, Panama, the West Indies, and northern South America.

BOCAS DEL TORO: Colón I, SW of Bocas del Toro at Macaw Hills, *von Wedel 526* (MO).

Known only from a single collection in Panama, *Hyptis atrorubens* has been characterized as a widespread tropical weed (Epling, 1937)—its paucity in this area may be due to poor collecting. Superficially, it resembles *H. lantanaefolia,* but lacks the pilose-annulate condition of the calyx tube associated with the latter species.

13. **Hyptis capitata** Jacq., Coll. **1:** 102, 1787.

Mesosphaerum capitatum (Jacq.) O. Ktze., Rev. Gen. Pl. **2:** 525, 1891.
Hyptis capitata var. *pilosa* Briq., Ann. Conserv. Jard. Bot. Genève **2:** 224, 1898.

Fig. 8. *Hyptis atrorubens* Poit.: A, habit (ca × 1); B, flower (ca × 6); C, stamens (ca × 10); D, nutlets (ca × 10). Probably after *von Wedel* 526 (MO).

Herbs, perennial, sparsely pubescent, to 2 m. *Leaves* ovate to ± rhomboid, acute, irregularly serrate, the bases obtuse to ± attenuate, to 12 cm long and 6 cm wide, glabrous to sparsely pubescent; subsessile to petioles ca 2-3 cm long. *Inflorescences* capitula, densely-flowered, axillary, 2-3 cm in diam, the peduncles ca 2-7 cm long; the bracts ovate-lanceolate, ca 5-7 mm long, sparsely pubescent, frequently reflexed and hidden at maturity. *Flowers* sessile; calyx tubular, ca 6-8 mm long at maturity, membranaceous, pilose-annulate within above the nutlets, sometimes only sparsely so, teeth spinulose, ca 1.5-2 mm long; corolla tube ca 3-3.5 mm long, white, the lower lip larger, ca 1 mm long, pubescent; stamens exserted, the filaments ± glabrous, the anthers ca 0.2 mm long. *Nutlets* (3-)4, ovoid, the lobes of the gynobase adhering, ca 1-1.2 mm long, pale to dark brown, the pericarp ± smooth.

A common weed of the American tropics, from Mexico to Colombia and Venezuela and west to Peru and Ecuador.

BOCAS DEL TORO: region of Almirante, *Cooper 82* (F). CANAL ZONE: Barro Colorado I, Fairchild Pt, *Ebinger 284* (MO); *Wetmore & Abbe 59* (F); Barro Colorado I, nr Laboratory, *Wetmore & Abbe 172* (F). CHIRIQUI: vic of Boquete, *Woodson & Schery 798* (MO). COCLE: s. loc., *Blum & Tyson 1888* (MO); El Valle de Antón, *Lewis et al. 2527* (MO). DARIEN: vic of Santa Fé, *Duke 9489* (MO); vic of Mannene, *Kirkbride & Bristan 1585* (MO); vic of Tucuti, *Terry & Terry 1402* (MO); Punta Mala, *Tyson 2716* (MO); Tonosí, on river bank, *Tyson et al. 2998* (MO). LOS SANTOS: vic of headwaters of Río Pedrogal, *Lewis et al 2970* (MO). PANAMA: Isla del Rey, *Duke 9522* (MO), *9567* (MO); E slope of Cerro Jefe, *Tyson 3414* (MO). SAN BLAS: mainland opposite Ailigandí, *Lewis et al. 69* (MO).

14. **Hyptis lantanaefolia** Poit., Ann. Mus. Hist. Nat. Paris **7:** 468, *t. 29, f. 1,* 1806.

Mesosphaerum lantanifolium (Poit.) O. Ktze., Rev. Gen. Pl. **2:** 525, 1891.

Herbs, perennial, procumbent to ± erect, to 1.5 m, incanous in the upper parts. *Leaves* ovate-elliptic, acute, crenate-serrate, the bases attenuate, sparsely pubescent above, the hairs appressed on veins beneath; sessile to petioles ca 0.5 cm long. *Inflorescences* capitula, densely-flowered, axillary, the peduncles to 4 cm long, the bracts ovate, sometimes broadly so, 5-7 mm long, the margins crenate. *Flowers* sessile, tufts of hair at the bases; calyx funnelform-tubular, the tube ca 1.5-1.8 mm long, pilose-annulate within above the nutlets, the teeth spinulose, ca 2.5-3.0 mm long; corolla tube ca 4-5 mm long, white or sometimes pale pink, the lower lip ca 2 mm long, pubescent; stamens ± included in the lower lip, the filaments pubescent near the base, the anthers ca 0.3 mm long; style exserted or included in the lower lip. *Nutlets* (3-)4, ovoid, pale brown, ca 1 mm long.

A common herb of grassland areas, and widely distributed from Mexico south to Sao Paulo, Brazil, west to Bolivia, and also in the West Indies.

CHIRIQUI: vic of Boquete, *Woodson & Schery 795* (MO). COCLE: El Valle, *Duyer 1823* (F, MO). PANAMA: Cerro Campana, *Duke 8660* (MO), *Ebinger 915* (MO), *McDaniel 6816* (MO); San José I, Bald Hill, *Johnston 46* (MO); nr Arraiján, *Woodson et al. 1405* (MO).

15. **Hyptis savannarum** Briq., Ann. Conserv. Jard. Bot. Genève **2:** 216, 1898.
Mesosphaerum savannarum Briq., loc. cit., pro syn.

Herbs, perennial, coarse, to 3 m, ± glabrous. *Leaves* lanceolate-ovate, the upper ± lanceolate, acute, serrate, the bases obtuse or attenuate, to 13 cm long and 4 cm wide, sparsely pubescent on the veins, resin-dotted; ± sessile. *Inflorescences* capitula, dense, axillary, ± globose at maturity, the peduncles 2.5-5 cm long, the bracts lanceolate or awl-shaped, ca 1 cm long, ± glabrous. *Flowers* ± sessile; calyx tubular-campanulate, ca 3-3.5 mm long at maturity, pilose-annulate within above the nutlets, the teeth acicular, ca 3-3.5 mm long, pubescent between; corolla tube ca 6-7 mm long, white and purple, the lower lip ca 1.5-2 mm long, lightly pubescent; stamens exserted, the filaments lightly pubescent, the anthers ca 0.4 mm long; ovary 4-lobed, the gynobase slightly elongated, becoming lobed, the style minutely bifid near the tip. *Nutlets* 4, oblong-flattened, the lobes of the gynobase sometimes adhering, ca 1.5-1.7 mm long, brown.

Guatemala, El Salvador, Costa Rica, Panama, Colombia, and Peru.

PANAMA: vic of Pacora, *Allen 1005* (MO); Cerro Campana, SE slope, *Lewis et al. 3134* (MO).

Hyptis savannarum is closely related to *H. conferta* and can be confused with it, especially with the narrow-leaved forms of the latter. However, the larger flowers and more spherical capitula, as well as the glabrous bracts of *H. savannarum* provide characters that easily distinguish it from *H. conferta.*

16. **Hyptis conferta** Pohl ex Benth., Lab. Gen. et Sp. 112, 1833.
Mesosphaerum confertum (Pohl ex Benth.) O. Ktze., Rev. Gen. Pl. **2:** 526, 1891.
Hyptis constricta Briq., Ann. Conserv. Jard. Bot. Genève, **2:** 217, 1898.

Herbs, perennial, coarse, to 1.5 m, appressed-pubescent on the branches. *Leaves* lanceolate or narrowly elliptical (in Panama), acute, serrate, the bases attenuate, to 18 cm long and 2.5 cm wide, glabrous or densely soft-pubescent above, glabrous or pubescent on the veins beneath, the midrib and secondary veins pronounced; sessile to petioles ca 0.5 cm long. *Inflorescences* capitula, dense, axillary, ± hemispherical, the peduncles ca 1-4 cm long, the bracts lanceolate or awl-shaped, ca 8-9 mm long, densely pubescent. *Flowers* sessile, tufts of hairs at the bases; calyx tubular-campanulate, ca 3-4 mm long at maturity, pilose-annulate within above the nutlets, the teeth acicular to setaceous, ca 3-4 mm long; corolla tube ca 4.5-5 mm long, white and rose, the lower lip ca 1.5-1.8 mm long, the lips and tube lightly pubescent; stamens exserted, the filaments sparsely pubescent near the base, the anthers ca 0.4 mm long; gynobase somewhat elongated, becoming lobed, the style minutely bifid near the tip. *Nutlets* 4, oblong-flattened, the lobes of the gynobase adhering, ca 1.5-1.6 mm long, brown.

A common species in the American tropics, found mostly at lower elevations, from Mexico to southern Brazil, and west to Bolivia.

CHIRIQUI: Boquete, *Pittier 2862* (GH). PANAMA: rd betw Chepo and Panama, *Dodge et al. 16648a* (MO); savanna nr Río Pacora and Chepo Hwy, *Duke 5911* (GH).

5. MARSYPIANTHES

Marsypianthes Mart. ex Benth., Lab. Gen. et Sp. 64, 1833.

Herbs prostrate or erect, often somewhat viscid. *Leaves* opposite, simple, petiolate, pinnately-nerved, membranaceous or rugose, generally dentate. *Inflorescences* capitula, loosely-flowered and pedunculate, or rarely flowers solitary, the bracts linear-lanceolate to ± ovate or awl-shaped. *Flowers* sessile or shortly pedicellate; bracteoles not apparent; calyx campanulate or funnelform, ± actinomorphic, with 5 ± equal lobes, lanceolate to deltoid; corolla tubular, bilabiate, the upper lip 2-lobed, the lower lip prominently 3-lobed, the middle lobe saccate; stamens 4, paired, mounted near the top of the corolla throat, decurved into the lower saccate lip, the filaments short, distinct, the connective not developed, the anthers with 2 functional thecae; ovary 4-lobed, the gynobase unlobed, the style bifid near the tip, the branches ± even. *Nutlets* 4, attached laterally to a columnar extension of the gynobase and ± open along this line at maturity.

Three species in tropical and subtropical America: *M. chamaedrys* in the West Indies and Mexico, south to Brazil and Peru; and two closely related species, *M. montana* Benth. (including *M. foliolosa* Benth.) from Brazil and *M. hassleri* Briq. from Paraguay and Brazil.

Useful reference:

Epling, C. C. Supplementary notes on American Labiatae. VII. Brittonia **12:** 140-150, 1960.

1. **Marsypianthes chamaedrys** (Vahl) O. Ktze., Rev. Gen. Pl. **2:** 524, 1891.—Fig. 9.

Clinopodium chamaedrys Vahl, Symb. **3:** 77, 1794.

Herbs, annual, prostrate or semi-erect, to 0.7 m, glandular-viscid and often with attached grains of sand or dirt. *Leaves* ovate, acute, crenate-serrate, the bases obtuse, subtruncate or cordate, to 7 cm long and 2 cm wide, both surfaces sparingly villous but often viscid; petioles ca 1-2.5 cm long. *Inflorescences* capitula, ± loosely flowered, peduncles ca 1-2.5 cm long, the bracts lanceolate, sometimes lanceolate-ovate, ca 8-10 mm long, fimbriolate. *Flowers* sessile or with pedicels to ca 2 mm long; calyx campanulate, ca 6-8 mm long at maturity, persistent, 10-ribbed, pubescent, membranaceous, the teeth deltoid; corolla tubular, purple, ca 7-9 mm long, bilabiate, the upper lip 2-lobed, the lower 3-lobed, the lips weakly pubescent; filaments pubescent, the anthers ca 0.5 mm long; style slender, ca 2-4 mm long, the stigma 2-lobed, the one acute. *Nutlets* (3-)4, ca 2 mm long, pale brown.

Mexico, Central America, the West Indies, south to Brazil and Peru.

CANAL ZONE: Coco Solo, US Army Trop Test Center, Mine Emplacement Center, *Dwyer & Duke 7909* (MO). CHIRIQUI: Boquete, *Davidson 603* (MO); llanos betw Boquete & David, *Ebinger 746* (MO). PANAMA: Cerro Campana, *Duke 5995* (MO); Altos del Río Pacora, *Lewis et al. 2354* (MO).

6. SCUTELLARIA

Scutellaria L., Sp. Pl. 598, 1753.

Herbs, mostly perennials, or half shrubs, erect or procumbent, rarely climbers, glabrous or pubescent. *Leaves* simple, opposite, petiolate or subsessile, pinnately-

Fig. 9. *Marsypianthes chamaedrys* (Vahl) O. Ktze.: A, habit (× ½); B, flower (ca × 5); C, nutlets (ca × 12); D, stamens (ca × 8). Specimen unknown.

nerved. *Inflorescences* verticillasters, or flowers solitary and opposite, or irregularly placed in the axils of bracts, the bracts leaf-like and persistent or deciduous. *Flowers* generally pedicellate; bracteoles usually apparent; calyx ± saccate, membranaceous, bilabiate, the lips entire, rounded and becoming concave, the upper

lip deciduous and usually with a transverse squama becoming an erect scutellum at maturity, the lower lip persistent; corolla tubular, bilabiate, generally long-exserted, red, orange, yellow, blue, violet, or white and one of the previous colors, the tube cylindrical and ± sigmoid, arcuate, or more sharply bent, the upper lip cup-shaped or galeate and ± joined obliquely to the lateral lobes of the lower lip, glabrous or pubescent within or without; stamens 4, paired, included in the upper lip, the pairs attached at different levels on the corolla tube, the filaments distinct, the connective not developed, the lower anthers with 1 functional theca; ovary 4-lobed, gynobase generally conspicuous and asymmetrical, variously described or functioning as a gynophore, the style long and slender, bifid near the tip, the upper style branch small or not apparent. *Nutlets* ca 3-4, attached at the base, ± ovoid or spherical, the pericarp variously tubercular or verrucose, sometimes provided with a band near the equator.

A large genus of ca 180 species found in most parts of the world. In the New World it ranges from the Arctic Circle to Tierra del Fuego and is represented by about 110 species. The number of species found in Panama is uncertain; Epling in the original manuscript cited only *S. glabra* Leonard, but there are at least two, and possibly four, additional species.

Scutellaria is probably the most distinctive genus in the *Labiatae*, chiefly because of the peculiar structure of the calyx, the squama or scutellum, (well-developed in all but 4 or 5 species), which, although easily seen at anthesis, becomes very exaggerated in fruit. Epling (1942) considers *Scutellaria* as singularly homogeneous for its size and distribution. He bases the sections largely upon characters more often associated with specific differentiation, which then becomes correspondingly tenuous. Specimens must have mature flowers, since corolla length is a constant character in Epling's keys both to sections and species. For this reason two collections cannot be identified: *Stern et al. 1031* (MO), from Chiriquí, has only two immature flowers and ambiguous vegetative characters; *Lewis et al.* 3522 (MO), from the Province of Panama, lacks corollas and although similar to *S. purpurascens* Swartz does not appear to be conspecific with it.

Useful references:

Epling, C. C. The American species of *Scutellaria*. Univ. Calif. Publ. Bot. **20:** 1-146, 1942.

Leonard, E. C. The North American species of *Scutellaria*. Contr. U.S. Natl. Herb. **22:** 703-748, 1927.

a. Subshrubs, robust; at least some leaves > 12 cm long . . . . . 1. *S. glabra*
aa. Herbs or shrubs; leaves < 8 cm long.
b. Herbs; leaves deltoid-ovate; corolla 12-15 mm long . . . . . 2. *S. purpurascens*
bb. Shrubs; leaves elliptic; corolla 20-25 mm long . . . . . 3. *S. lewisiana*

1. **Scutellaria glabra** Leonard, Contr. U.S. Natl. Herb. **22:** 715, 1927.

Subshrubs, erect, to 1.5 m, mostly glabrous. *Leaves* ovate or elliptic-ovate, subentire or undulate, the bases shallowly cordate, to 18 cm long and 8 cm wide, glabrous; petioles ca 3-5 cm long. *Inflorescences* verticillasters, 1-2-flowered, arranged in a false raceme, ca 10-25 cm long, the bracts lanceolate, ca 3-5 mm

Fig. 10. *Scutellaria glabra* Leonard: A, habit (× ½); B, flower (ca × 2.5); C, stamens (ca × 2.5); D, nutlets (× 5). After *White 106* (MO).

long, early deciduous. *Flowers* with pedicels ca 2-6 mm long; bracteoles 2, minute, < 0.5 mm long; calyx 2.5-3 mm long in flower, enlarging to ca 5-6 mm in fruit, the squama of the upper lip extending to ca 4-5 mm in fruit; corolla red or blue, ca 2-2.5 cm long, the tube constricted above the calyx, then weakly expanded, the upper lip arched, the lower lip flat, naked within; lower stamen pair attached 13-15 mm from the base, the anthers ca 0.6 mm long; gynobase conspicuous, asymmetrical and gynophore-like, the style long and slender, the branches unequal. *Nutlets* (3-)4, semi-spherical, black, evenly tuberculate, ca 2 mm in diameter.

CHIRIQUI: upper Chiriquí Viejo Valley, trail from Paso Ancho to Monte Lirio, *Allen 1478* (MO); Chiriquí Viejo Valley, *White 106* (MO).

2. **Scutellaria purpurascens** Swartz, Prodr. 89, 1788.

Herbs, perennial, erect or somewhat decumbent, to 40 cm, short-pubescent throughout. *Leaves* deltoid-ovate, acute, ± crenate, the bases rounded or shallowly cordate, to 7 cm long and 4 cm wide, sparsely pubescent to glabrous above, pubescent on the veins beneath; petioles to 3 cm long. *Inflorescences* verticillasters, mostly 1-flowered, the bracts lanceolate and ciliate, 2-4 mm long. *Flowers* with pedicels to 6 mm long at maturity; bracteoles 2, minute, ca < 0.5 mm long; calyx 2 mm long in flower, ca 4-5 mm long in fruit, the squama then 4-5 mm long, sparsely and minutely pubescent; corolla blue, 12-15 mm long, naked within or very sparsely pubescent; lower stamen pair attached 6-8 mm from the base; gynobase conspicuous and asymmetrical, the style apparently unlobed. *Nutlets* (2-)4, ± spherical, brown, ca 1.5-1.7 mm in diameter.

The Lesser Antilles, Costa Rica, Panama, Colombia, Venezuela, and Brazil.

BOCAS DEL TORO: Sixola Valley, Sibubi Falls, *Rowlee & Rowlee* 378 (NY). CANAL ZONE: Garden at Gatun Station, *Hayes* 59 (NY). DARIEN: 0-4 mi up Río Sabana from Santa Fé, *Duke 4135* (MO); Caná & vic, *Williams 764* (NY), 949 (NY).

3. **Scutellaria lewisiana** Nowicke, Phytologia (in press).—Fig. 11.

Shrubs, the upper stems maroon and with curled pubescence. *Leaves* elliptic, acute, serrate, the bases obtuse, to 6 cm long and 2 cm wide, glabrous, resin-dotted, dark-green above, pale green beneath; petioles ca 1-2 cm long. *Inflorescences* verticils, 2-flowered, ca 1 cm distant, arranged in a false raceme, the bracts elliptic, ca 3-4 mm long. *Flowers* with pedicels ca 4-6 mm long; bracteoles 2, 0.5 mm long; calyx ca 4 mm long in flower, softly pubescent; corolla ca 23-25 mm long, lavender, the lower lip white, ± straight, lightly pubescent; lower stamen pair attached on the upper half of the corolla tube, the anthers ca 0.6 mm long; gynobase conspicuous, asymmetrical, the style unlobed. *Nutlets* unknown.

CHIRIQUI: Caldera-Chiriquicito trail, betw Quebrada Hondo and Divide, *Kirkbride & Duke 920* (holotype MO).

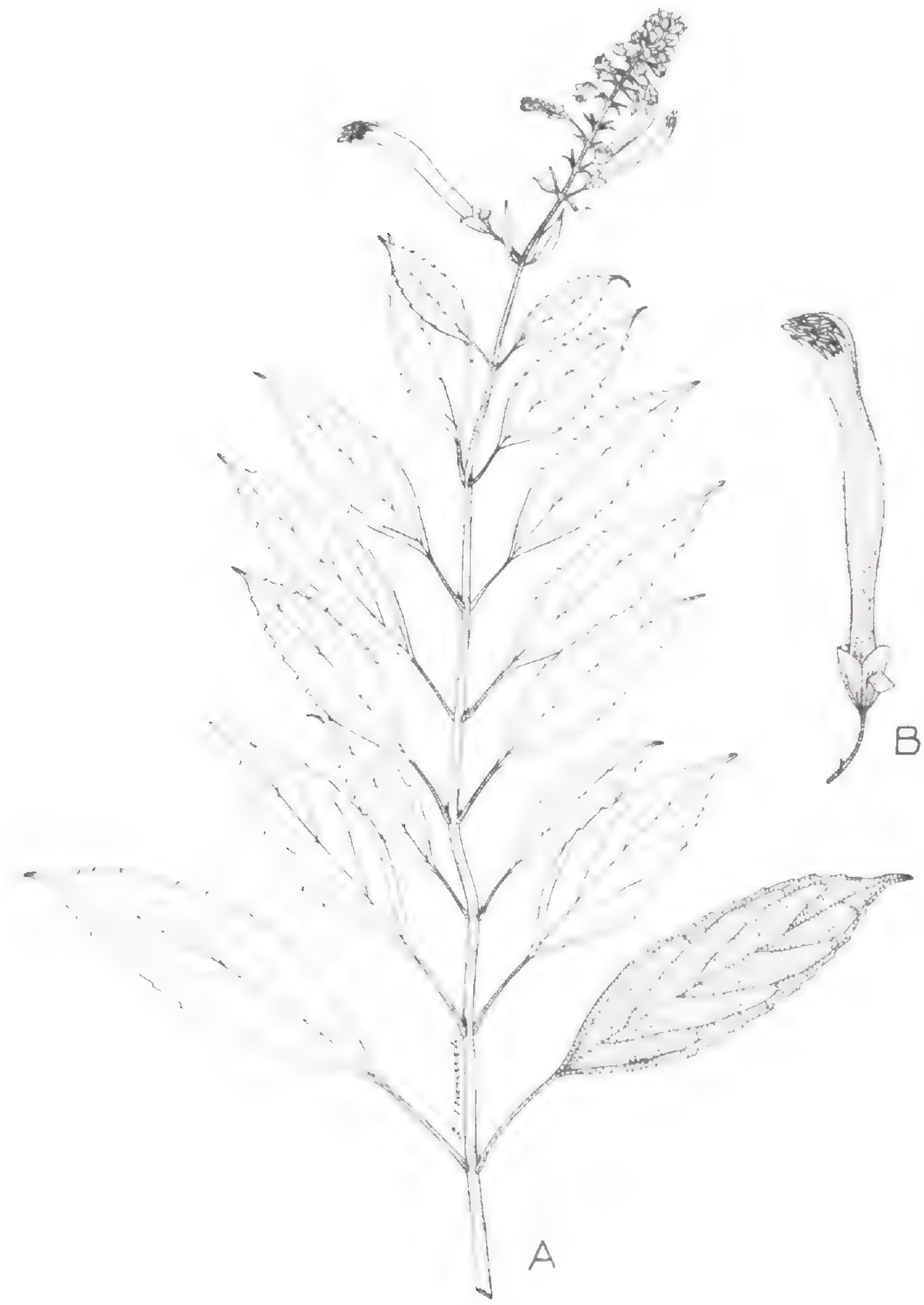

Fig. 11. *Scutellaria lewisiana* Nowicke: A, habit (ca × 5/7); B, flower (ca × 2). After *Kirkbride & Duke 920* (MO).

7. OCIMUM

Ocimum L., Sp. Pl. 597, 1753.

Herbs, annual or perennial, or small shrubs, the stems glabrous or pubescent. *Leaves* opposite, simple, pinnately-nerved, mostly petiolate. *Inflorescences* verticils, ca 6-flowered or sometimes 10-flowered, appearing overall as a spike or a raceme, the bracts leaf-like. *Flowers* mostly pedicellate; bracteoles not apparent; calyx ± campanulate, frequently deflexed in fruit, bilabiate, the upper lip ± entire, rounded, the margins decurrent partially or completely to the base of the calyx tube, the lower lip 4-toothed, the teeth aristate and unequal; corolla tubular, enclosed or exserted, bilabiate, the upper lip 4-lobed, the lower entire and flat or concave; stamens 4, paired, equal to the corolla tube or exserted, the filaments distinct, the upper pair naked, the lower pair glabrous or pubescent, with or

without an appendage at the base, the anthers with 2 functional thecae; ovary 4-lobed, the gynobase lobed or unlobed, the lobes sometimes as high as the nutlets at anthesis, the style slender, bifid near the tip, the branches equal or unequal. *Nutlets* ca 4, attached at the base, ± spherical, the pericarp smooth or warty.

Commonly called Basil, the genus consists of about 50 to 60 species in the warmer regions of the world.

An unusual representation in Panama with the presence of *O. gratissimum* L. as well as the widespread weeds *O. micranthum* Willd. and *O. americanum* L., and the apparent absence of *O. basilicum* L., the most frequently cultivated species.

a. Lower stamen pair with naked filaments; mature calyx 7-9 mm long, the decurrent margins of the upper calyx lobe extending to the base ..... 1. *O. micranthum*
aa. Lower stamen pair with pubescent or appendaged filaments, calyx ca < 6 mm long at maturity, the decurrent margins of the upper calyx lobe not extending completely to the base.
  b. Herbs < 0.5 m; leaves < 2 cm wide, subentire; calyx pubescent at the base with stiff hairs ca 2 mm long, the decurrent margins of the upper lip extending almost to the base ..... 2. *O. americanum*
  bb. Subshrubs, to 2 m; leaves > 3 cm wide, ± crenate; calyx softly pubescent at the base, the decurrent margins of the upper lip ca 1/3 to 1/2 as long as the calyx ..... 3. *O. gratissimum*

1. **Ocimum micranthum** Willd., Enum. Hort. Berol. 630, 1809.—Fig. 12.

Herbs, annuals, erect to 1 m, the branches cymose-divaricate, glabrous. *Leaves* rhomboid, obovate or ovate, acute, serrate, the bases attenuate, to 7.5 cm long and 3.5(-5 in the type) cm wide, resin-dotted, ± glabrous to lightly pubescent on the veins; petioles to 4 cm long. *Inflorescences* verticils, each ca 6-flowered, 0.5-1.5 cm distant, the false raceme to 15 cm long, bract leaf-like, ca 4-6 mm long. *Flowers* with pedicels ca 4-5 mm long, pubescent; calyx 7-9 mm long at maturity, membranaceous, pubescent on the veins, the upper lobed rounded, 3-veined, margins decurrent on the calyx tube to its base, the lower ca 6-8-veined, teeth upwardly curved; corolla tubular, ca 3-4 mm long, the upper 4-lobed, the lower entire; filaments naked, the anthers ca 0.5 mm long; ovary 4-lobed, gynobase ± unlobed, the style slender, ca 3-4 mm long, the branches unequal. *Nutlets* (3-)4, ca 1.7-2.0 mm long, the pericarp dark brown, minutely warty.

Widely distributed in the American tropics.

BOCAS DEL TORO: Old Bank I, *von Wedel 1865* (MO); Colón I, *von Wedel 2838* (MO). CANAL ZONE: Miraflores Lake, *White 199* (MO). DARIEN: Yaviza, along Quebrada Uvital off Río Chucunaque, *Duke 4999* (MO); Campamento Buena Vista, *Stern et al. 814* (MO). HERRERA: Pesé, *Allen 803* (MO); Ocú, *Allen 4090* (MO). LOS SANTOS: 3 mi S of Carreta, *Burch et al. 1249* (MO). PANAMA: sabanas nr Chepo, *Hunter & Allen 68* (MO). SAN BLAS: Mulatuppu, *Duke 8481* (MO), *8522* (MO); Pino I, *Elias 1719* (MO); mainland opposite Ailigandí, *Lewis et al. 74* (MO).

2. **Ocimum americanum** L., Amoen. Acad. **4:** 276, 1759.

O. canum Sims, Bot. Mag. **51:** *t. 2452,* 1824.
O. stamineum Sims, loc. cit.

Herbs, annuals, to 40 cm, pubescent with uniseriate curled hairs. *Leaves* elliptic, acute, subentire, the bases obtuse, to ca 3 cm long and 1 cm wide, sparingly pubescent above, more so on the veins beneath, resin-dotted; petioles ca

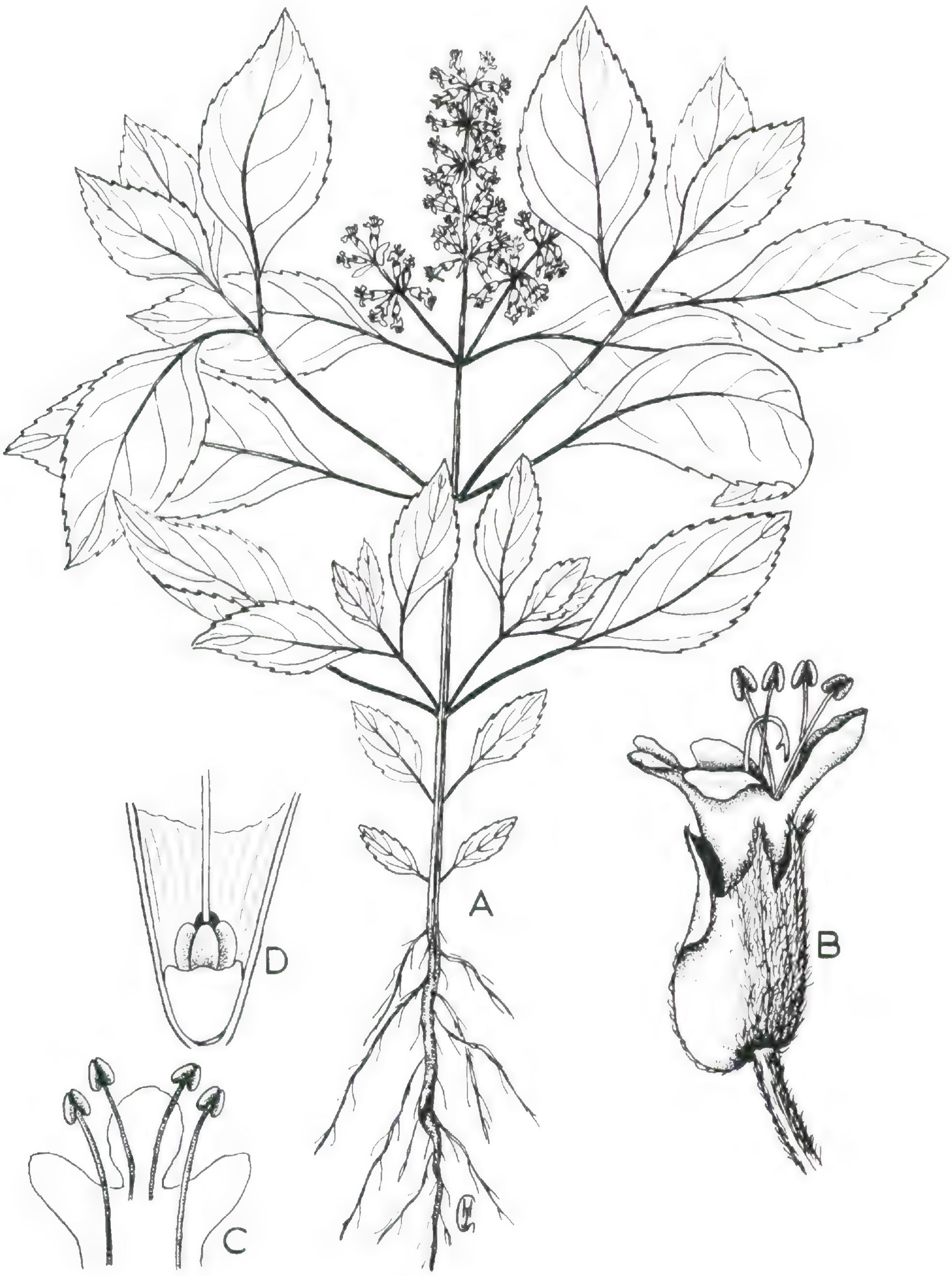

Fig. 12. *Ocimum micranthum* Willd.: A, habit (ca × ½); B, flower (ca × 10); C, stamens (ca × 8); D, nutlets (ca × 15). Specimen unknown.

0.5-1 cm long. *Inflorescences* verticils, ca 6-flowered, 1-1.5 cm distant, the false raceme to 17 cm long, the bracts elliptic, ca 3.5-4.5 mm long, the margins pubescent. *Flowers* with pedicels ca 2-2.5 mm long; bracteoles not apparent; calyx 4-5 long at maturity, pubescent within and without at the base, the hairs ca 2 mm long, the upper lip rounded and acutely tipped, 3-veined, the decurrent margins extending almost to the base, the lower lip 5-7-veined, the lateral teeth wider; corolla tubular, white to yellow-green, the tube ca 2-3 mm long, the lips ca 1-1.5 mm long, the lower lip ± concave; stamens exserted, the lower pair with a small appendage at the base of the filament, the anthers ca 0.6 mm long; ovary 4-lobed, the gynobase lobed, the style bifid near the tip, the branches ± equal. *Nutlets* (3-)4, oblong, ca 1.2 mm long, black, the pericarp ± warty.

Frequent in the American tropics.

DARIEN: headwaters of Río Chico, specimen cultivated by Choco Indians, *Allen 4627* (MO).

3. **Ocimum gratissimum** L., Sp. Pl. 1197, 1753.

Subshrubs, erect, to 2 m, glabrous to softly pubescent on the younger branches. *Leaves* ovate or elliptic, acute, crenate to subentire, the bases rounded and weakly attenuate or ± obtuse, to 7 cm long and 4.5 cm wide, resin-dotted, glabrous above and sparsely pubescent on the veins beneath; petioles to ca 4.5 cm long, pubescent. *Inflorescences* verticils, each ca 6-flowered, 0.5-1 cm distant, the false racemes 10-15 cm long, the bracts ± deltoid, 2-3 mm long, pubescent. *Flowers* with pedicels ca 1-2 mm long; bracteoles not apparent; calyx 3-4 mm long, membranaceous, resin-dotted, pubescent on the veins and at the base, naked within, the upper lip entire, 3-veined, lateral margins decurrent only on upper ⅓ of tube, the lower lip 5-7-veined; corolla tubular, white and purple, ca 2.5 mm long overall; stamens exserted, lower filament pair with conspicuously pubescent appendages at the base, the anthers ca 0.6 mm long; ovary 4-lobed, gynobase weakly lobed, the style bifid near the tip, the branches ± equal. *Nutlets* (3-)4, ± spherical or slightly elongated, ca 1.2 mm long, the pericarp warty.

The tropics of America and Africa, and Ceylon, Java, and the East Indies.

VERAGUAS: Canazas, *Tyson 3651* (MO).

8. TEUCRIUM

Teucrium L., Sp. Pl. 562, 1753.

Herbs, perennial, rarely annual herbs or half-shrubs, branching from the base or in the inflorescences. *Leaves* opposite or whorled, simple or variously lobed or parted, petiolate or subsessile, pinnately-nerved. *Inflorescences* verticillasters, 1-∞ flowered, solitary and axillary, or arranged in spikes, the bracts leaf-like. *Flowers* subsessile or with slender pedicels; bracteoles not apparent; calyx tubular or campanulate, sometimes becoming saccate at maturity, actinomorphic or weakly zygomorphic, 10-veined, the teeth ± equal, or the lower tooth larger; corolla tubular and short, or funnelform and slightly exserted, scarcely bilabiate, seemingly 1-lipped and 5-lobed, in actuality the upper lip 2-lobed, the lobes laterally

placed, the lower lip 3-lobed, the middle lobe largest, the 2 lateral lobes about equal to the lobes of the upper lip; stamens 4, paired, exserted, the lower pair longer, the filaments distinct, the connective not developed, the anthers with 2 functional thecae; ovary 4-lobed, the style terminal, long and slender, bifid near the tip. *Nutlets* ca 4, temporarily united, ovoid to wedge-shaped, glabrous or pubescent, the pericarp sculptured or smooth.

A ± cosmopolitan genus of 100 species with a center of distribution in the Mediterranean area; one species has been collected in Panama.

Useful reference:

McClintock, E., and C. C. Epling. A revision of *Teucrium* in the New World, with observations on its variation, geographical distribution, and history. Brittonia **5**: 491-510, 1946.

1. **Teucrium vesicarium** Mill., Gard. Dict. ed. 8, 1768.—Fig. 13.

Herbs, perennials, to 1 m, rootstocks creeping, pubescent with curved hairs or with spreading ± glandular hairs. *Leaves* opposite, ovate or oblong-ovate, acute, crenate-serrate, rounded or subtruncate at the base, to 7 cm long and 3.5 cm wide, the upper surfaces pubescent or glabrous, the lower paler with soft curved hairs, or ± glabrous, sometimes with longer straight hairs on the veins; petioles ca 2-2.5 cm long. *Inflorescences* verticillasters, 1-flowered, arranged as a terminal spike, to ca 17 cm long, the bract leaflike, lanceolate, ca 4-6 mm long, pubescent beneath. *Flowers* with pedicels ca 1 mm long; calyx weakly bilabiate, 5-7 mm long, the upper lip 2-toothed, the lower lip 3-toothed, the teeth deltoid, pubescent, inflated and ± saccate at maturity; corolla tubular, exserted or equal to the calyx, the upper small and inconspicuous, the lower ca 4 mm long; stamens 4, exserted, the anthers 0.5 mm long. *Nutlets* wedge-shaped, glabrous, wrinkled, 2-2.5 mm long.

A variable species in tropical America.

BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *von Wedel 1668* (MO); Nievecita, 50 m, *Woodson et al. 1857* (MO).

9. LEPECHINIA

Lepechinia Willd., Hort. Berol. **1**: 21, 1803.

Sphacele Benth. in Edwards, Bot. Reg. **15**: *pl. 1289*, 1829.

Herbs, half-shrubs, or shrubs. *Leaves* opposite, simple, generally petiolate, pinnately-nerved. *Inflorescences* verticils, loosely or densely flowered, arranged in open or crowded spikes, or sometimes reduced to a single flower, the bracts leaf-like. *Flowers* sessile or pedicellate; bracteoles generally not apparent; calyx campanulate, ± actinomorphic to weakly bilabiate, ca 10-veined, often membranaceous, enlarging at fruiting time, the teeth sometimes conivent; corolla tubular to campanulate, enclosed or shortly exserted, white, blue, or purple, naked within or a ring of hair-like appendages near the base, weakly bilabiate, the upper lip weakly 2-lobed, the lower 3-lobed, the lobes ± flat; stamens 4, paired, the filaments distinct, the connective not developed, the anthers with two functional thecae, the thecae

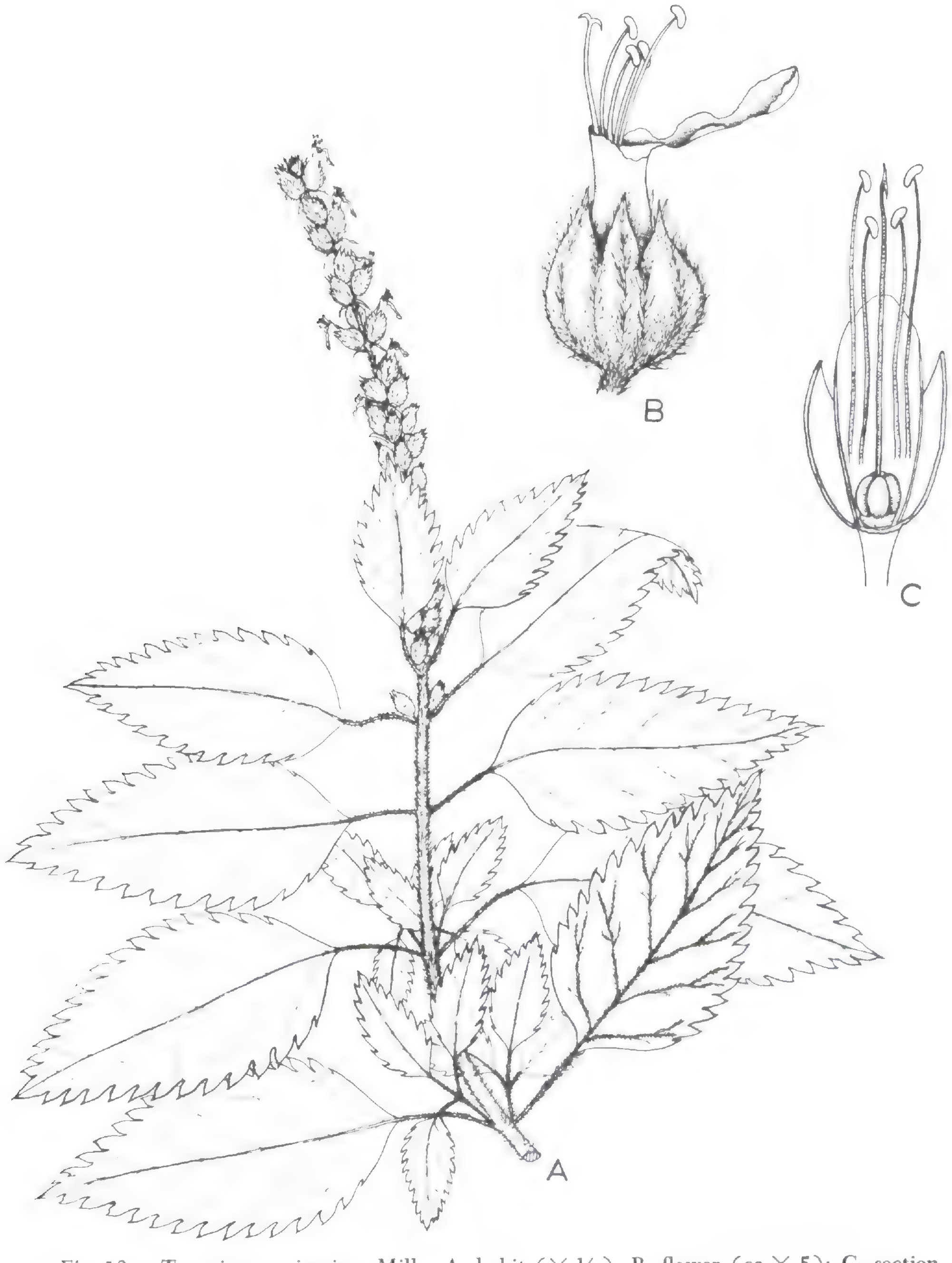

Fig. 13. *Teucrium vesicarium* Mill.: A, habit (× ½); B, flower (ca × 5); C, section of flower with stamens and nutlets (ca × 5). After *von Wedel 1668* (MO).

diverging or parallel; ovary 4-lobed, the gynobase generally uniform and thick, the style gynobasic, bifid near the tip, the branches ± flattened or awl-shaped. *Nutlets* 4, attached at the base, ovoid, black or brown, smooth or puberulent.

Lepechinia is a predominantly New World genus of about 38 species, ranging from California to Chile. Epling (1935) reduced *Sphacele* Benth, to *Lepechinia* and removed *Dekinia* Mart. & Gal., which Briquet (*Labiatae,* Naturl. Pflanzenfam. IV 3: 183-375, 1897) had included in his treatment of the genus.

Useful reference:

Epling, C. C. A synopsis of the tribe *Lepechinieae (Labiatae).* Brittonia **6:** 352-364, 1948.

1. **Lepechinia schiedeana** (Schlecht.) Vatke, Verh. Bot. Vercins Prov. Brandenburg **17:** Sitzungsber. 36, 1875.—Fig. 14.

Stachys schiedeana Schlecht., Linnaea **7:** 398, 1832.

Herbs, procumbent, the stems ca 20-40 cm long, pubescent throughout, the hairs uniseriate. *Leaves* elongate-deltoid, acute, the bases truncate-cordate, to 5 cm long and 2 cm wide, pubescent on both surfaces, densely so beneath, the upper surface rugose-areolate; subsessile to petioles to 6 cm long on basal leaves. *Inflorescences* verticils, each 6-flowered, crowded at anthesis, becoming remote at fruiting, the bracts leaf-like, enlarging with maturation. *Flowers* with pedicels 2-3 mm long; bracteoles not apparent; calyx campanulate, 4-6 mm long in flower, enlarging to 10-11 mm in fruit, reticulate between the veins, membranaceous, pubescent at anthesis, weakly bilabiate, the upper lip 3-toothed, the lower 2-toothed, the teeth ca equal in length or the lower teeth slightly shorter; corolla ca 4-5 mm long, blue or purple, a ring of hair-like appendages near the base; stamens slightly exserted, the thecae ± diverging; gynobase present, the style lobes somewhat flattened. *Nutlets* (3-)4, ovoid, ca 1.8-2 mm long, the pericarp reticulate.

Central America.

CHIRIQUI: Cerro Copete, summit and SW slope, *Allen 4887* (MO); Volcán de Chiriquí, Potrero Muleto to summit, *Woodson & Schery 428* (MO).

10. STACHYS

Stachys L., Sp. Pl. 580, 1753.

Herbs, annual or perennial, rarely half shrubs or shrubs, usually pubescent. *Leaves* simple, opposite, pinnately-nerved, petiolate or subsessile. *Inflorescences* verticils, 4-∞ flowered, appearing as spikes, the bracts leaf-like or absent. *Flowers* perfect, subsessile or shortly pedicellate; bracteoles generally apparent; calyx weakly zygomorphic, the teeth subequal and frequently aristate or spinulose-tipped; corolla tubular, exserted or included, purple to pink, the tube frequently constricted above the nutlets, sometimes with a spur on the lower side, bilabiate, the upper lip subgaleate and 2-lobed, the lower lip 3-lobed, the central lobe largest, sometimes with a pilose annular ring above the nutlets; stamens 4, paired, slightly exserted or inclosed in the upper lip, the filaments distinct, glabrous or pubescent, the connective not developed, the anthers with 2 functional thecae, the thecae strongly divergent or parallel; ovary 4-lobed, the gynobase unlobed or forming a nectarium, the style bifid near the tip, the branches equal and acute. *Nutlets* ca 4, attached at the base, ± obovate.

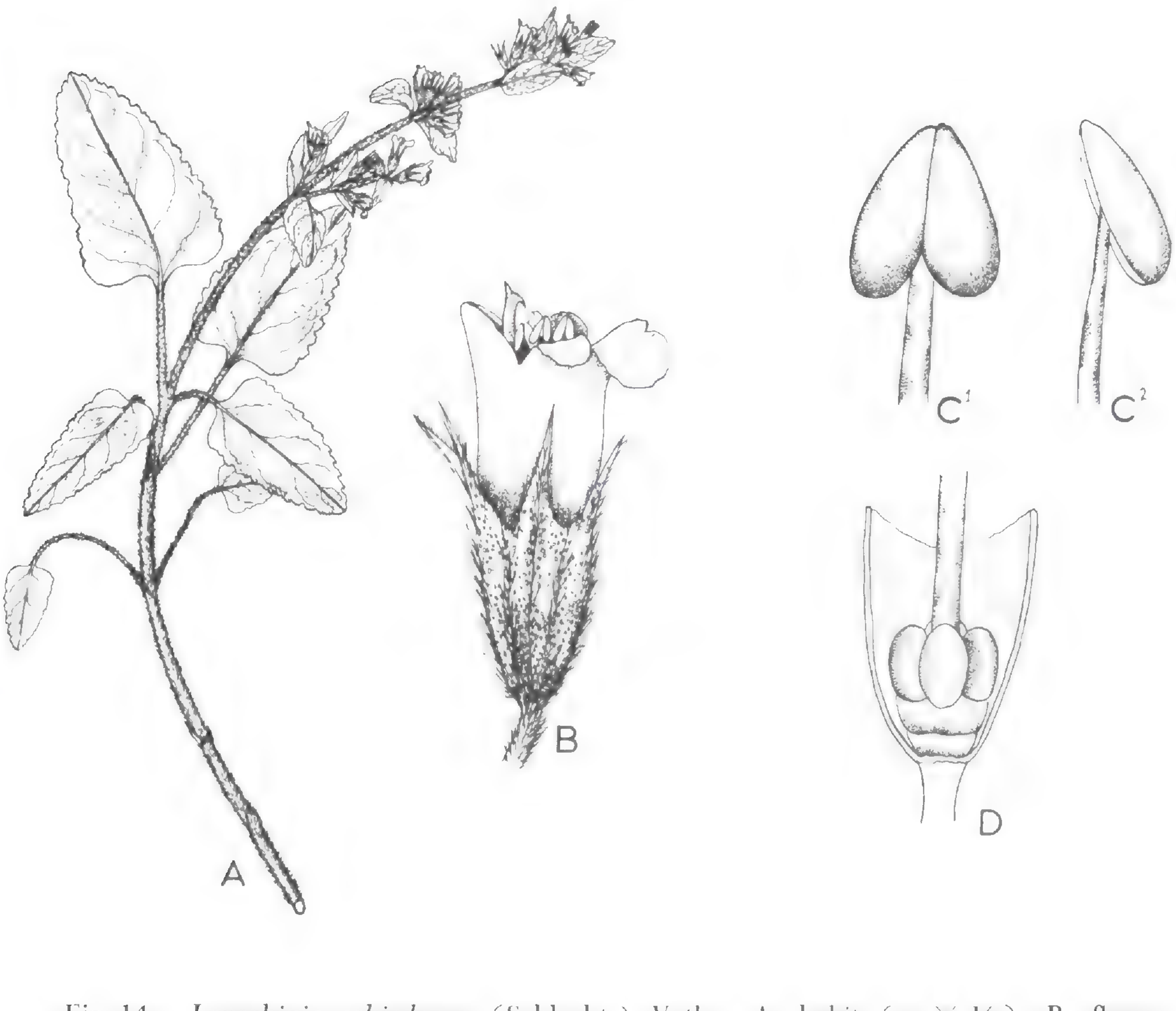

Fig. 14. *Lepechinia schiedeana* (Schlecht.) Vatke: A, habit (ca × ½); B, flower (× 7); C¹, anther top view (ca × 15), C², anther side view (ca × 15); D, nutlets (ca × 10). After *Woodson 1036* (location unknown).

Up to 200 species in the North Temperate Zone and extending to South America and South Africa.

Useful reference:

Epling, C. C. Preliminary revision of American *Stachys*. Repert. Spec. Nov. Beih. **80:** 1-75, 1934.

1. **Stachys costaricensis** Briq., Bull. Soc. Roy. Bot. Belgique **30:** 240, 1891.—Fig. 15.

Herbs, prostrate, rooting at the nodes, the younger branches sparsely pubescent, the hairs uniseriate and ± retrorse. *Leaves* ovate to elongate-deltoid, acute, crenate-serrate, the bases ± truncate, ca 3-5 cm long and ca 2-3.5 cm wide, sparsely pubescent on both surfaces and on the margins; petioles ca 1.5-3 cm long, sparsely pubescent. *Inflorescences* verticils, ca 6-flowered, appearing as spike-like racemes, ca 5-10 cm long, the bracts lanceolate, ca 6-10 mm long, reflexed, or the lowermost verticil in the axils of reduced leaves. *Flowers* subsessile; bracteoles

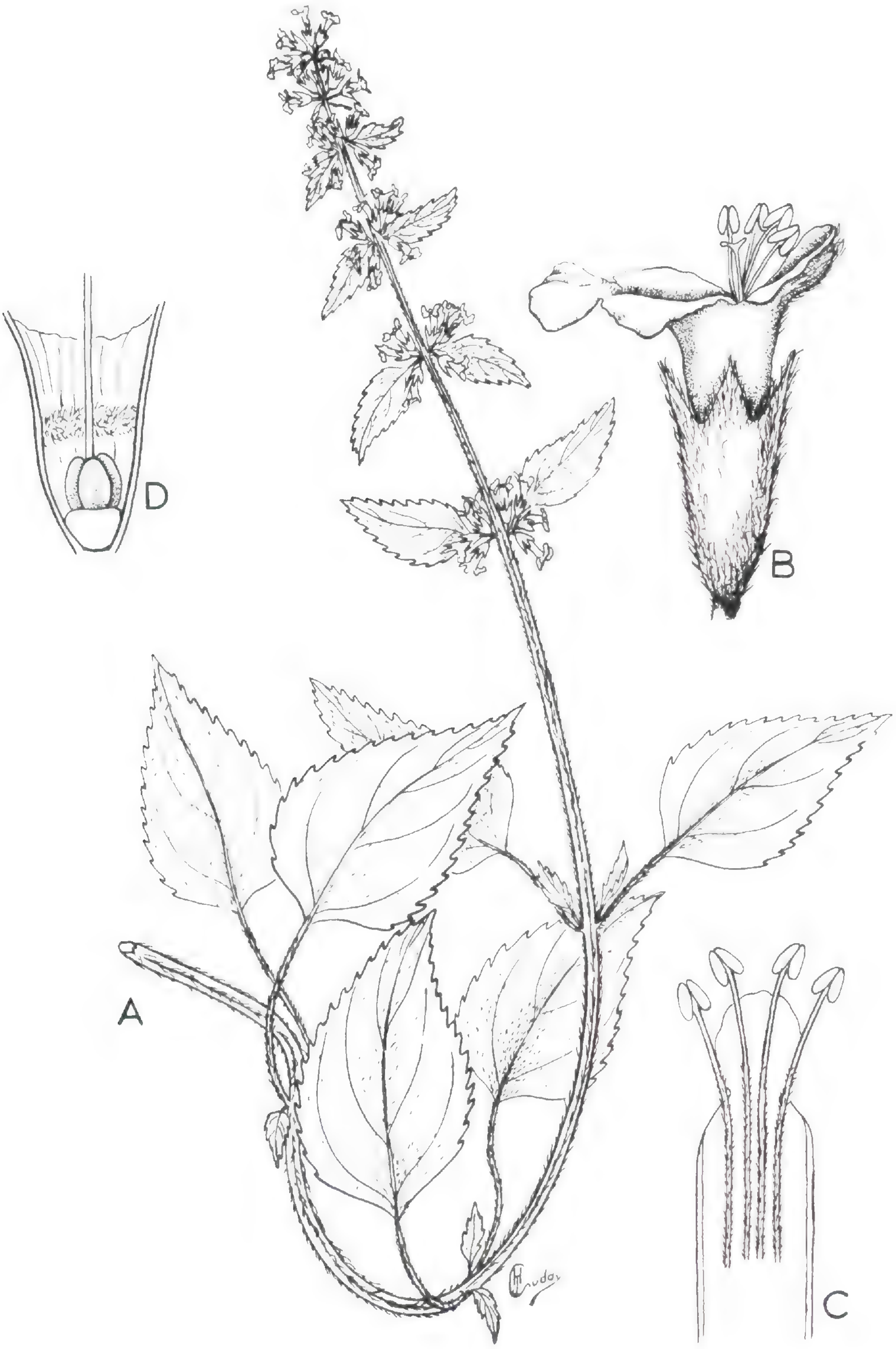

Fig. 15. *Stachys costaricensis* Briq.: A, habit (ca × 1); B, flower (ca × 8); C, stamens (ca × 10); D, nutlets (ca × 5). After *Woodson & Schery* 552 (MO).

present, awl-shaped, ca 1-2 mm long, pubescent; calyx campanulate, weakly zygomorphic, the tube ca 2-3 mm long at maturity, the teeth deltoid-lanceolate, ca 2 mm long, pubescent, obscurely nerved but each tooth apex with a spine-like tip, the uppermost largest; corolla tubular, 5-6 mm long, ± pink, constricted ca halfway up and with a small spur on the lower side, the upper lip 2-lobed and concave, ca 2-3 mm long, the lower lip 3-lobed and spreading, ca 3-4 mm long, pubescent within and without, annular-pubescent within near the constriction; stamens exserted, the filaments pubescent, the anthers ca 0.5 mm long; ovary 4-lobed, the gynobase unlobed, the style glabrous, bifid near the tip, the branches ± equal. *Nutlets* ca 4, ovoid, ca 1-2 mm long, dark brown.

Mexico and Central America.

CHIRIQUI: nr Boquete, *Pittier* 2966 (location unknown, acc. Epling, 1934); vic of Bajo Mono & Quebrada Chiquero, 1500 m, *Woodson & Schery* 552 (MO).

INDEX OF LATIN NAMES

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

Ballota suaveolens 86
Clinopodium chamaedrys 97
Coleus **83**
  blumei **83**
Cunila **81**
  polyantha **81,** 83†
Dekinia 108†
Hyptis 72†, **84,** 84†
  atrorubens **93,** 93†
  brachiata **93**
  brevipes **91**
  capitata **93**
  — var. pilosa 93
  conferta 96†, **96**
  constricta 96
  crenata var. augustifolia 90
  dilatata **90**
  lantanaefolia 93†, **95**
  mutabilis **87**
  oblongifolia **88**
  obtusiflora **91**
  pectinata **86**
  pulegioides **87**
  recurvata **88**
  savannarum **95,** 96†
  suaveolens **86**
  verticillata **85**
  vulcanica 88
Labiatae 72†, 73†, 84†, 99†, 108†
Lepechinia **104,** 108†
  schiedeana **106**
Lepechineae 108†
Marsypianthes **96**
  chamaedrys 97†, **97**
  foliolosa 97†
  hassleri 97†
  montana 97†
Mesosphaerum 84
  atrorubens 93
  brachiatum 93
  brevipes 91
  capitatum 93
  confertum 96
  dilatatum 90
  lantanifolium 95
  mutabile 87
  oblongifolium 88
  obtusiflorum 91
  pectinatum 86
  pulegiodes 87
  recurvatum 88
  savannarum 95
  suaveolens 86
  verticillatum 85
  vulcanicum 88
Nepeta
  mutabilis 87
  pectinata 86
Ocimum **102**
  americanum 103†, **103**
  basilicum 103†
  canum 103
  gratissimum 103†, **105**
  micranthum 103†, **103**
  stamineum 103
Salvia 72†, **72,** 73†, 78†, 81†
  albopileata 80, 81†
  alvajaca **78**
  compacta 77
  — var. irazuensis 76
  hyptoides **75**
  irazuensis 76
  longimarginata 73†, **77**
  membranacea **76,** 77†
  — var. villosula 76
  micrantha **74**
  occidentalis **74,** 74†
  orbicularis 74
  ourophylla 78
  permixta 78
  polystachya **77,** 77†
  psilophylla 78, 78†
  pteroura **76**
  tiliaefolia 73†
  tonduzii 80
  trichopes **78,** 78†
  wagneriana **80**
Scutellaria **97,** 99†
  glabra 99†, **99**
  lewisiana 101
  purpurascens 99†, **101**
Sphacele 106, 108†
Stachys **108,** 109†
  costaricensis **109**
  schideana 108
Teucrium **105,** 106†
  vesicarium **106**

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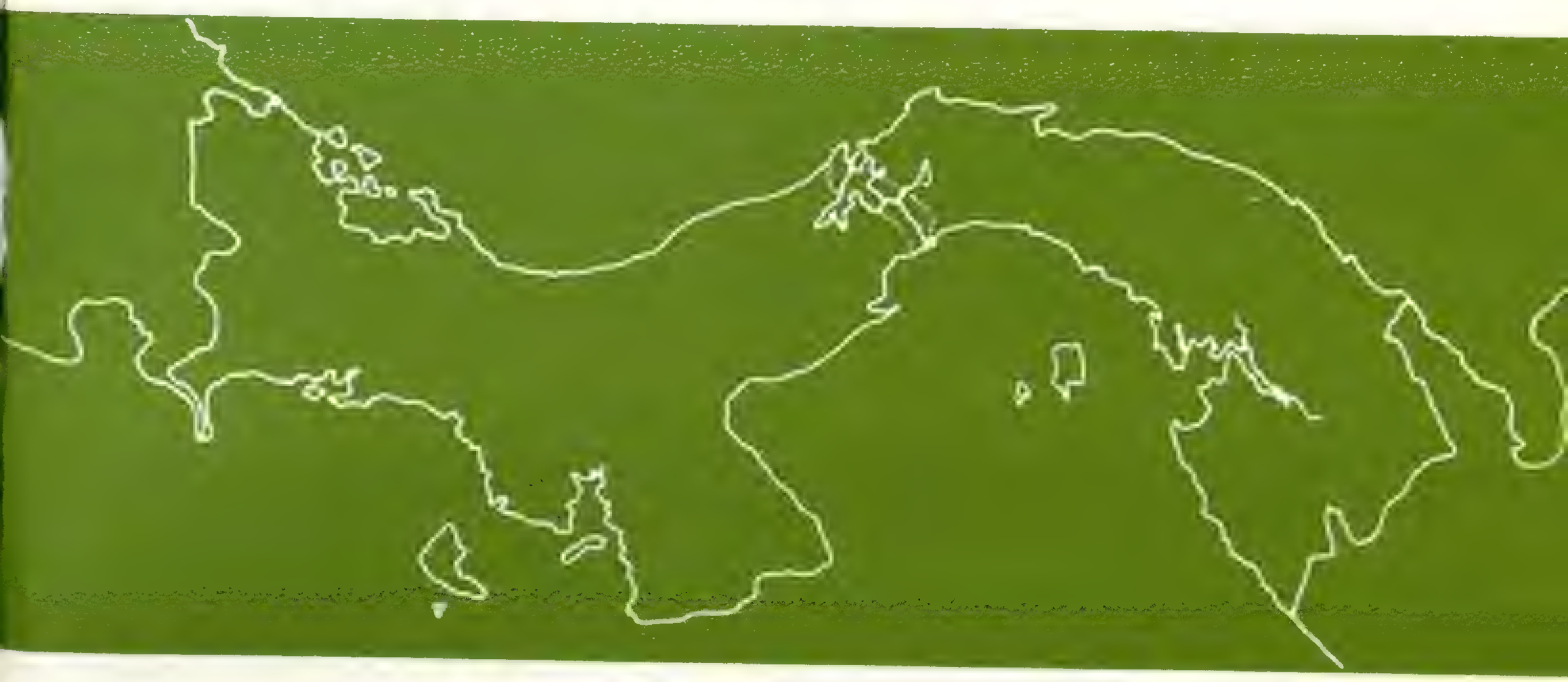

CONTENTS

Viable Soil Algae from the Herbarium of the Missouri Botanical Garden *Bruce C. Parker, Noel Schanen & Richard Renner* 113

Scanning Electron Microscopy as an Aid to Pollen Taxonomy *John E. Ridgway & John J. Skvarla* 121

On Tropical Tree Seedlings. I. Seeds, Seedlings, Systems, and Systematics *James A. Duke* 125

Adventive Plants New to the Missouri Flora (III) *Viktor Muehlenbach* 163

Notes on the Galápagos Euphorbieae (Euphorbiaceae) *Derek Burch* . 173

The Genus *Cienfuegosia* Cav. (Malvaceae) *Paul A. Fryxell* . . . 179

The Initiation of Vascular Cambium and Production of Secondary Xylem in Flower Bud Pedicels of *Asclepias curassavica* L. *F. M. Safwat* . . 251

Cytological and Chromatographic Evidence of Interspecific Hybridization in *Petalostemon* *Sally A. Walker* 261

The Genus *Hoffmannia* (Rubiaceae) in Panama *John D. Dwyer* . . 269

NOTES

The Skunk Cabbage in Missouri *Erna R. Eisendrath* 287

Supplementary Notes on the Phytolaccaceae, I. *Joan W. Nowicke* . 288

Kallstroemia (Zygophyllaceae) in Missouri *Duncan M. Porter* . . 290

VOLUME 56
1969
NUMBER 2

ANNALS OF THE
Missouri Botanical Garden

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ANNALS OF THE
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VIABLE SOIL ALGAE FROM THE HERBARIUM OF THE MISSOURI BOTANICAL GARDEN

BY
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St. Louis

ABSTRACT

Soil particles from herbarium sheets of aquatic, bog and terrestrial plants were used as innoculum on Bold's modified Bristol's medium. Forty-six of the 124 innoculations were successful, and algae were obtained from specimens up to 60 years old. Green algae were the most frequent survivors from plants collected within the last 30 years, and blue-greens from the period before that.

INTRODUCTION

Although many have recognized the importance of desiccation resistence to survival of microorganisms (Evans, 1959; Hortobagyi, 1960; Lund, 1962), few investigators have approached this question through attempts to culture algae from soil samples kept dry in excess of a few years.

Bristol (1919) identified 11 genera (7 blue-green, 3 green, 1 diatom) which grew from 16 samples of partially air-dried English soils sealed in lead-capped bottles for 23-70 years. Algae and fungi developed even in the 70-year-dry soil when moistened with Bristol's inorganic salt solution and placed in light for some months.

Lipman (1941) attempted to grow algae from fragments of numerous herbarium sheets of green and blue-green algae. The only culture which developed was a specimen of *Nostoc commune* collected in 1853. Lipman repeated this experiment twice, establishing a record viability of 86 and 87 years for this species.

Becquerel (1942) took dry soil from 10 non-disinfected herbarium specimens of various mosses and fern allies spanning 56-98 years in age. When placed in sterile inorganic salts medium (pH 5) of unreported composition in window light, 14 different genera ultimately developed (4 blue-green, 9 green, 1 diatom). All

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soils yielded viable algae including the 98-year-old sample from which the diatom *Nitzschia palea* grew.

In contrast to these reports, Parker (unpublished) failed to obtain viable algae from numerous herbarium specimens of lichens 35 to more than 100 years old following mild surface sterilization of the plant fragments.

We know of no efforts besides these to treat directly the longevity of algae or population viability under drought conditions. Therefore, we set out during 1967-'69 to examine more extensively the questions treated by Bristol (1919), Lipman (1941), and Becquerel (1942).

METHODS

Using the herbarium of the Missouri Botanical Garden (MO), we obtained, after much searching, 50 specimens of bog or aquatic vascular plants dating from 1831 to 1966 on which small crumbs of dry soil remained. A second series comprising 74 specimens of *Gramineae* (mostly terrestrial) dating from 1885 to 1966.

Unlike the herbaria used by Lipman (1941) and Becquerel (1942), all our source material except the 1966 *Gramineae* had received some kind of disinfection. At least back to 1955, all plants at MO were fumigated with carbon tetrachloride, naphthalene and paradichlorobenzene before mounting. Before this time formaldehyde or mercuric chloride were used. After filing, the specimens are continuously subject to the vapors of the same chemicals used for the initial fumigation.

We picked dry soil crumbs no more than a few millimeters in diameter from roots with ethanol-flamed forceps and placed them aseptically into 50-ml cotton-plugged Erlenmeyer flasks or Pyrex screw-cap test tubes, both approximately half full of sterile Bold's (1949) modified Bristol's medium. Cultures were developed in approximately 3000 lux of constant, cool-white fluorescent light at 22-23° C, then placed in subdued light. After approximately two months, containers with visible growth were examined microscopically to determine the taxonomic affiliation of the viable algae. We made no attempts to identify all algae to species or genus level, a task now requiring elaborate sub-culturing and specialized skills for many groups (Bold & Parker, 1962; Chantanachat & Bold, 1962; Bischoff & Bold, 1963; Brown & Bold, 1964; Cox & Bold, 1966; Koster, 1966; Smith & Bold, 1966; Pearson & Kingsbury, 1966; Allen & Stanier, 1968). As new cultures developed, they too were observed, allowing in most cases, nearly two years for the appearance of visible growth.

RESULTS

Although visible growth appeared as late as one year in a few cultures, most algae grew to maximum proportions within a few months. In all, 46 of the 124 soil crumbs yielded viable algae contrasting strikingly with results of Bristol (1919) and Becquerel (1942) who obtained viable algae from all their soil samples. Fungi developed in a greater number of cultures than did algae. Table 1 lists the algae which grew from the bog and aquatic plant series and from the predominantly terrestrial *Gramineae*.

TABLE 1. CHRONOLOGICAL LIST OF HERBARIUM SOURCE MATERIAL YIELDING VIABLE ALGAE. AQUATIC PLANTS (FIRST SERIES) AND GRAMINEAE (SECOND SERIES)

Date Collected	*Source Plant*	*Algae Identified*
12-18-66	*Limnocharis flava*	*Oscillatoria,* chlorococcacean, *Ulothrix (Uronema?)*
12-18-66	*Limnocharis flava*	*Oscillatoria,* chloroccacean, *Navicula*
5-27-62	*Alisma gramineum*	*Oscillatoria, Aulosira*
5- 5-55	*Isoetes melanopoda*	2 chlorococcacean spp.
3-11-51	*Equisetum hyemale*	chlorococcacean sp.
9-26-46	*Triglochin* sp.	*Phormidium?*
4-24-43	*Equisetum arvense*	2 chlorococcacean spp.
9-27-40	*Equisetum hyemale*	2 chlorococcacean spp.
5-26-38	*Equisetum ferrissii*	chlorococcacean sp.
7-23-35	*Typha latifolia*	*Nostoc*
4-14-35	*Equisetum hyemale*	*Nostoc*
7- 9-31	*Saggittaria umeata*	chlorococcacean sp.
1910	*Triglochin maritima*	*Nostoc*
12-24-66	Unidentified, unsterilized	*Lyngbya, Gleocystis* (or palmelloid chlorococcalean)
12-19-66	Unidentified, unsterilized	chlorococcacean, *Protosiphon*
12-14-66	Unidentified, unsterilized	chlorococcalean, *Protosiphon* and *Botrydium?*
12-14-66	Unidentified, unsterilized	*Oscillatoria,* chlorococcacean, *Scenedesmus*
12-13-66	Unidentified, unsterilized	chlorococcalean, chaetophoracean
12-12-66	Unidentified, unsterilized	chlorosphaeralean
12- 7-66	Unidentified, unsterilized	chlorosphaeralean, *Cylindrocapsa*
12- 7-66	Unidentified, unsterilized	*Anabaena, Lyngbya*
9-28-62	*Uniola laxa*	*Stigonema,* chlorococcalean, chlorosphaeralean
9- 4-62	*Panicum agrostoides*	*Protosiphon*
9- 2-62	*Manisaria rugosa*	*Protosiphon*
7-13-62	*Paspalum pubescens*	*Nostoc, Gloeocystis* (or palmelloid chlorococcalean), *Scenedesmus?*
9-30-61	*Echinochloa frunentacea*	chlorococcacean
9- 2-61	*Aristida wrightii*	chlorococcacean
9-17-60	*Trioda* sp.	2 chlorococcacean spp.
6-17-59	*Avena fatua*	chlorococcalean
6-24-57	*Stipa comata*	*Anabaena,* chlorococcacean
6- 6-57	*Bouteloua curtipendula*	*Anabaena*
6- 5-57	*Aristida wrightii*	chlorococcacean
8-10-55	*Panicum agrostoides*	chlorococcalean
8-22-53	*Echinochloa frumentacea*	chlorococcalean
4-28-53	*Splenophalis* sp.	*Trebouxia,* chlorococcalean, *Gloeocytis*
8- 6-51	*Calamogrostis epigejos*	chlorosphaeralean
8-23-49	*Calamogrostis canadensis*	chlorococcalean
5-29-48	*Panicum polyanthes*	*Hapalosiphon,* chlorococcalean
8-19-46	*Stipa columbiana*	chlorococcacean
7-13-46	*Andropogon virginicus*	*Nostoc*
7-11-45	*Stipa comata*	chlorococcacean
10- 3-43	*Bouteloua curtipendula*	*Chroococcus?,* chlorococcacean
8- 7-42	*Paspalum pubescens*	*Anabaena*
9-12-41	*Muhlenbergia setifolia*	chlorococcacean
6-27-40	*Panicum agrostoides*	chlorococcacean, chlorosphaeralean
9- 3-33	*Paspalum ciliatifolium*	*Anabaena*

These data illustrate that no alga survived more than 60 years. Green algae dominated in frequency of appearance during the most recent 30 years, while blue-green algae dominated the preceding 30-year period. Only one diatom grew and this from the most recent material. Our results show further that similar viabilities occurred for the aquatic plants as for the predominantly terrestrial ones. Although we did not identify species, it was clear that recent collections (1966) yielded a greater diversity of cytological strains (probably species) than older collections, especially the non-preserved *Gramineae*. Figure 1 illustrates the steady loss in viability of algal populations with increasing age of dried soil sample.

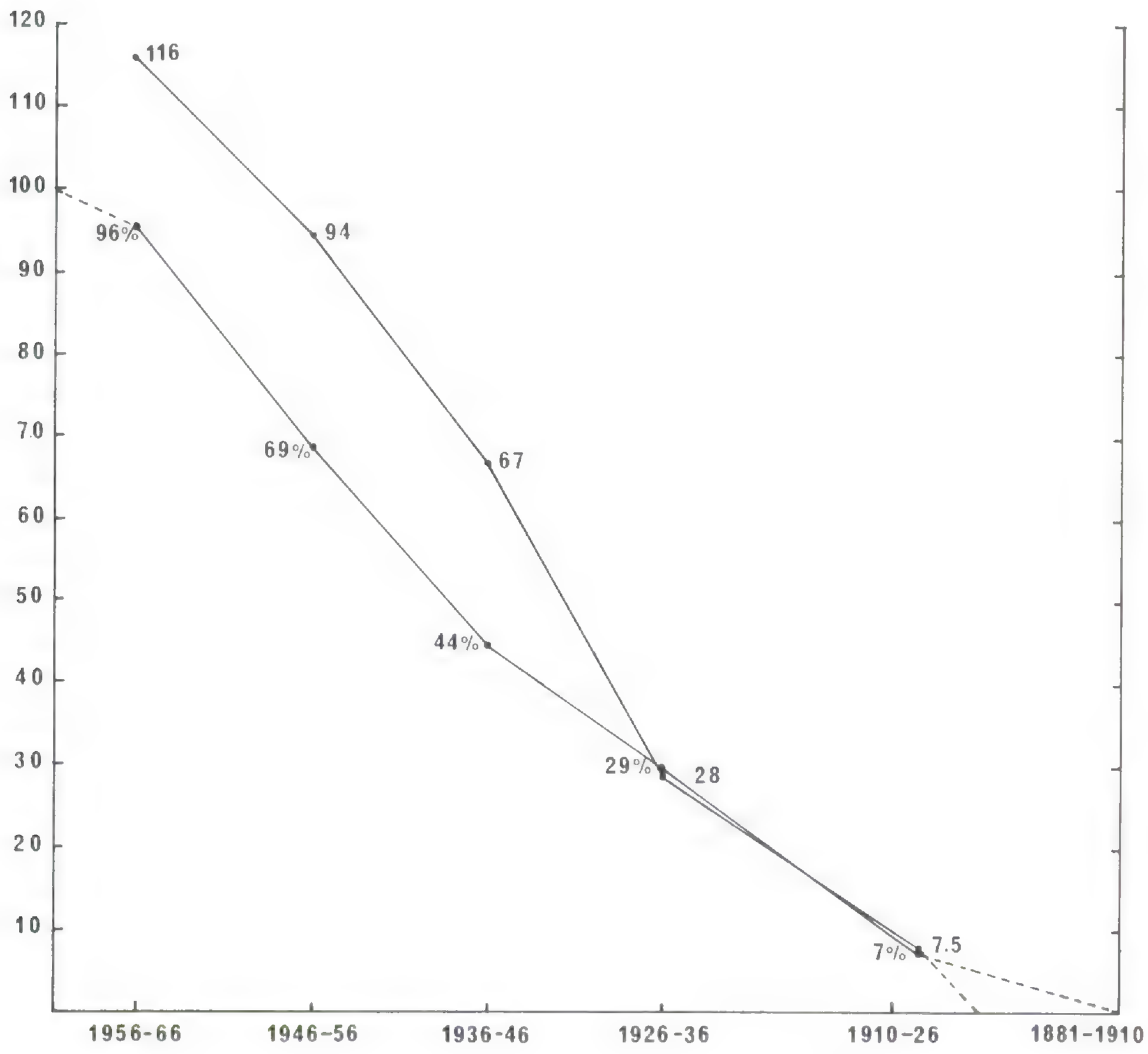

Fig. 1. Graph showing loss in algal viability, expressed in two ways: (1) as % of cultures developing algae; (2) as (Minimum No. Species Populations No. Cultures) × 100. For convenience, calculations were based on approximately 10-year periods as shown on abcissa.

Noteworthy among the genera not reported by earlier workers but found in our cultures were a chaetophoracean alga, *Cylindrocapsa, Scenedesmus, Ulothrix,* and *Navicula,* all from recent specimens, and the genus *Protosiphon* in somewhat older source material.

Among the blue-green algae, filamentous forms dominated in our cultures as with those of Bristol (1919) and Becquerel (1942), the *Nostocaceae* appearing most frequently. Among the green algae, unicellular chlorococcalean forms dominated in all these studies. Diatoms were of rare occurrence.

Discussion

We have confirmed the findings of Bristol (1919) and Becquerel (1942) that a variety of soil algae, mainly belonging to the Chlorophycota and Cyanophycota, remain viable in dry soil for several decades in sufficient numbers to regenerate a visible population in response to favorable growing conditions. Table 2 illustrates this fact and other details we shall discuss. Our data also agree with that of Lipman (1941) which suggested that blue-green algae, especially *Nostoc* and *Anabaena,* possess greater survival capacities than other algae.

That only one diatom grew in our cultures as well as those of Bristol (1919) and Becquerel (1942), may reflect partially the media employed. Neither Bristol's

Table 2. Frequency of Occurrence of Viable Algae (by genus) in Dry Soil Reported by Bristol (1919), Becquerel (1942) and Us.

Genus and Major Group	Bristol	Becquerel	Parker et al.
Cyanophycota:			
Anabaena	7	0	5
Aulosira	0	0	1
Chroococcus?	0	0	1
Cylindrospermum	2	0	0
Hapalosiphon	4	0	1
Lyngbya	0	0	2
Nodularia	1	0	0
*Nostoc**	11	1	5
Oscillatoria	—	1	4
Phormidium	1	0	1?
Plectonema	4	0	0
Siphononema	0	1	0
Stigonema	0	2	1
Chlorophycota:			
Botrydina	0	1	0
chaetophoracean sp.	0	0	1
chlorococcacean spp.	0	0	23
chlorococcalean spp.	0	0	9
Chlorococcum	11	1	0
chlorosphaeralean spp.	0	0	5
Coccomyxa	0	1	0
Cylindrocapsa	0	0	1
Dactylothece	0	1	0
Dictyococcus	0	1	0
Gloeocystis	0	0	3
Microcystis? (a green)**	0	1	0
Oocystis	0	1	0
Protosiphon	0	0	4
Scenedesmus	0	0	2
Stichococcus	4	3	0
Trebouxia (= *Cystococcus*)	0	4	1
Trochiscia	4	0	0
Ulothrix (*Uronema?*)	0	0	1
Chrysophycota:			
Botrydium?	0	0	1
Navicula	0	0	1
Nitzschia	1	1	0

* See also Lipman (1941) for record longevity.

** Becquerel's reference to this blue-green algal genus as a green alga renders its identity questionable.

(1919) medium nor Bold's (1949) modified Bristol's medium favors diatoms, and Becquerel (1942) did not describe the composition of his medium. Xanthophycean algae, however, grow satisfactorily in these media, so their absence suggests a low viability for this group in air-dried soil.

The pattern of reduced viability with increasing age of soil samples terminating at 1910 in our study lends credence to our assumption that our experimental technique was entirely sterile and that algal contamination of soil crumbs in this herbarium is infrequent. Bristol (1919) also took precautions to avoid contamination, but we are not as certain that Becquerel (1942) was equally careful to maintain sterile conditions. If the algae which developed in Becquerel's soil samples were of the same age as the source material (65-98 years), then we might conclude that some factor(s) brought about reduced maximum longevity of algae in our soil samples. For example, treatment of our herbaria with preservatives or differences in soil moisture contents might explain our apparent higher mortality. Indeed, Bristol's soil samples possessed moisture contents somewhat higher than most fully air-dried soils, and neither her soils nor those used by Becquerel were pretreated with carbon tetrachloride or continuous vapors from paradichlorobenzene and naphthalene.

Another possible explanation for the older soils of Bristol (1919) and Becquerel (1942) yielding viable algae is that they used larger amounts of soil in their inocula. Our soil crumb inocula, which were unusually small (1-3 mm) as a result of meticulous cleaning of herbarium mounted plants, may have contained significantly fewer viable algal cells initially. This feature would tend to produce a more steeply sloping mortality curve.

Bristol (1919) encountered blue-green algae more frequently than green algae, while we and Becquerel (1942) obtained the opposite result. This difference between our data and that of Bristol could have resulted from differences in media or soils. The salts in Bristol's medium are 4× the concentration of Bold's (1949) modified Bristol's medium, while the ratios of salts (e.g., sodium nitrate/potassium phosphate) are the same. One might postulate that, over a long enough period of time, moist soil will experience some dentrification via the mixed microbial community present, and the N/P ratio will drop. This ratio should drop more in Bristol's solution than in Bold's modified medium, because the phosphate level will remain essentially constant. Such a lower N/P ratio may have favored the development of nitrogen-fixing blue-green algae which dominated Bristol's cultures, especially following the appearance of green algae.

Our data demonstrates the remarkable ability of soil algal populations to survive for many years in an air-dry condition. We cannot conclude that individual algal cells live this long, because cell division might have occurred during the long holding period. At least, given sufficient moisture, some soil algae can reproduce in absolute darkness (Parker, 1961). However, we have assumed that algal cell division does not occur in dry soil and that the mortality of individual cells within a population may be considerable with but a few cells surviving many years. The importance of this feature to mechanisms of algal dispersal and survival over periods of drought can not be ignored.

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SCANNING ELECTRON MICROSCOPY AS AN AID TO POLLEN TAXONOMY[1,2]

BY JOHN E. RIDGWAY AND JOHN J. SKVARLA

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ABSTRACT

Information obtained from scanning electron microscopy of whole pollen grains of *Zea* and *Iva* indicates direct correlation with that gathered from light microscopy and electron microscopy of thin sections. This information helps clarify and support past analyses.

INTRODUCTION

The portrayal of pollen surfaces has been greatly improved by the scanning electron microscope. Although still a relatively new instrument, there are already several publications describing its utility in pollen and spore investigations (see Echlin, 1968, for an extensive bibliography).

For a number of years one of us (J.J.S.) has been concerned primarily with the morphology and taxonomy of grass and composite pollen. This has involved studies with the light microscope and the transmission electron microscope. Since the scanning electron microscope offers a rapid means of observing pollen wall surfaces, as well as providing greater resolution than the light microscope, the importance of this instrument to our work is obvious. Although preparative techniques for the scanning electron microscope are relatively simple and have been described (Echlin, 1968), comparatively little information is available on the two major processing techniques employed in taxonomic studies of pollen (viz. fresh and acetolyzed). Moreover, the aperture regions, so critical in taxonomic diagnoses, have been neglected at the expense of the unaperturate portions of the pollen wall. This report illustrates the effectiveness of scanning electron microscopy in studies of pollen morphology.

MATERIALS AND METHODS

Fresh pollen of *Zea mays (Gramineae)* and species of *Iva (Compositae)* were used. The pollen was examined in three stages: (1) fresh, unstained, (2) fresh, stained with OsO_4, and (3) acetolyzed. After OsO_4 staining or acetolysis, the pollen was dehydrated through graded alcohols and allowed to dry after final rinses in either propylene oxide or reagent grade acetone.

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[1] The authors wish to acknowledge use of the scanning electron microscope laboratory facilities, Department of Pathology, Washington University, as provided by the Health Sciences Advancement Award (NIH 1 SO4 FR 06115); and to Stemen Laboratories, Oklahoma City, for some of the pollen samples.

[2] Supported in part by a Pioneer Hi-Bred Corn Co. grant to J. E. Ridgway and by NSF grant GB-6768 to J. J. Skvarla.

Preparation for the scanning electron microscope consisted of dusting the dried pollen onto specimen stubs which held a piece of double-stick Scotch tape. The stubs were then placed in a Kinney vacuum evaporator and shadowed with chromium. During shadowing the stubs were continually rotated through 360 degrees. After 30 - 45 seconds of evaporation the pollen was ready for observation in the scanning electron microscope. A Stereoscan Mk IIa Scanning Reflection Electron Microscope was used to analyze the pollen.

RESULTS

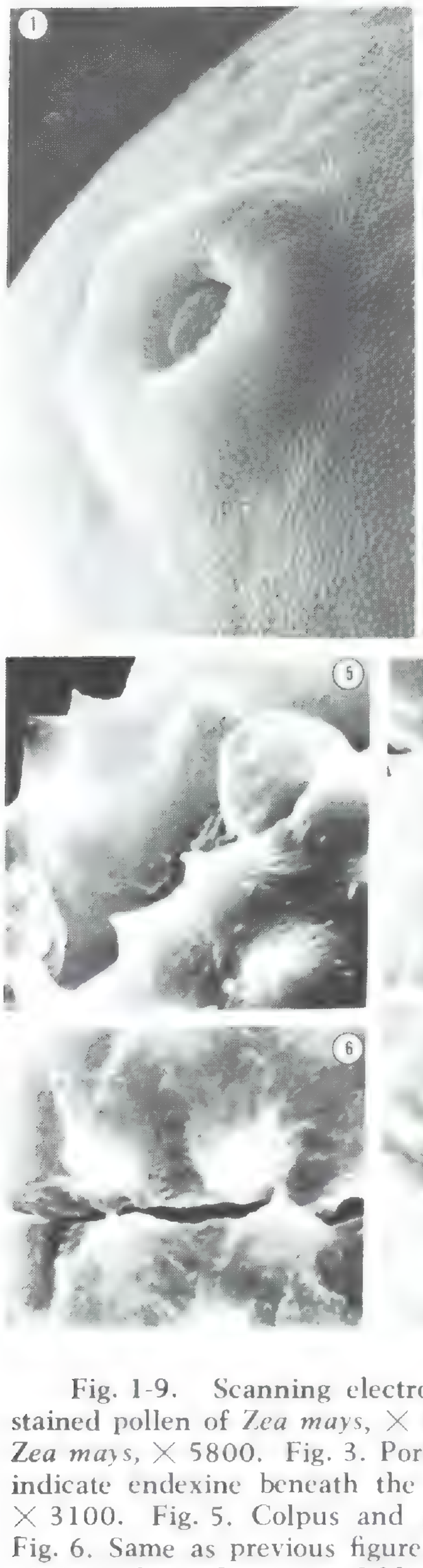
Zea mays. Fresh, untreated pollen showed a high percentage of wrinkled, collapsed and exploded grains. However, details of the pore region even in distorted grains proved to be instructive. In Figure 1 an essentially intact pore clearly shows the raised annulus surrounding a depressed operculum. The latter is ornamented with spinules which are similar to those present on the pollen surface. In Figure 2 the operculum is missing, probably due to the high vacuum environment during shadowing. The angle of tilt of this grain is such that a differentiation in electron conductance is evident along one portion of the pore circumference. This difference in pollen wall density is believed to reflect the bilayered nature of the pore. Such an interpretation is consistent with transmission electron microscope studies of thin sections (Skvarla and Larson, 1966).

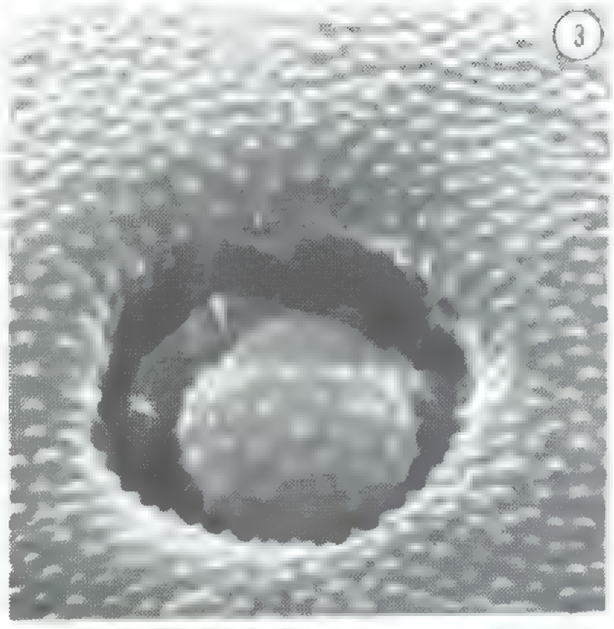
When fresh pollen was treated with OsO_4 for approximately 45 minutes the percentage of distorted grains was appreciably decreased. The preservation of the pore region, however, was not significantly improved and was comparable to fresh untreated grains. For example, the endexine layer which normally traverses the gap beneath the operculum and consequently is not visible in surface view, can, by virtue of operculum tearing, be clearly distinguished (Fig. 3).

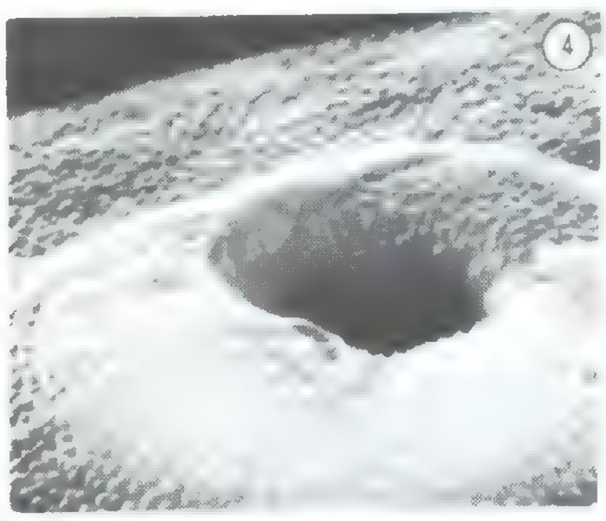
Acetolysis demonstrated a stability comparable to that achieved with OsO_4 treatment. Opercula were nearly always absent (due to acetolysis) but pore and exine details provided results identical to those by the above processing treatments (Fig. 4).

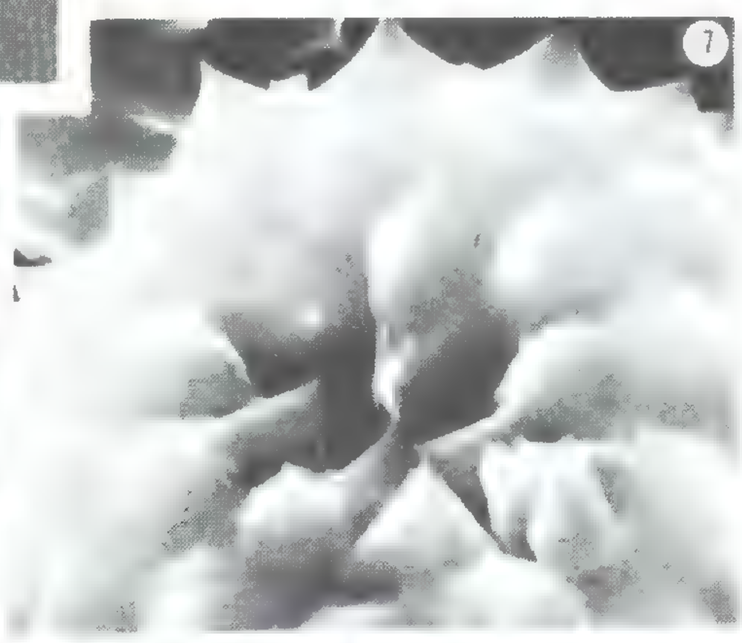
Iva. Composite pollen, because of its robust exine, is substantially more resistant than *Zea* to distortion during evaporation and in the electron beam. The greatest difficulty in working with this pollen was in analyzing grains with extensive colpi. In fresh, untreated *Iva xanthifolia* (Fig. 5) the colpus and pore were photographed almost immediately after initial observation. When a second exposure was attempted a few minutes later, the flanks of the colpus had become relaxed and closed (Fig. 6), thus obscuring the pore. This tendency of the colpus/pore region to fold inward was frequently noted in fresh untreated pollen (Fig. 7). With the application of a short OsO_4 treatment the colpus showed less of a tendency toward closing.

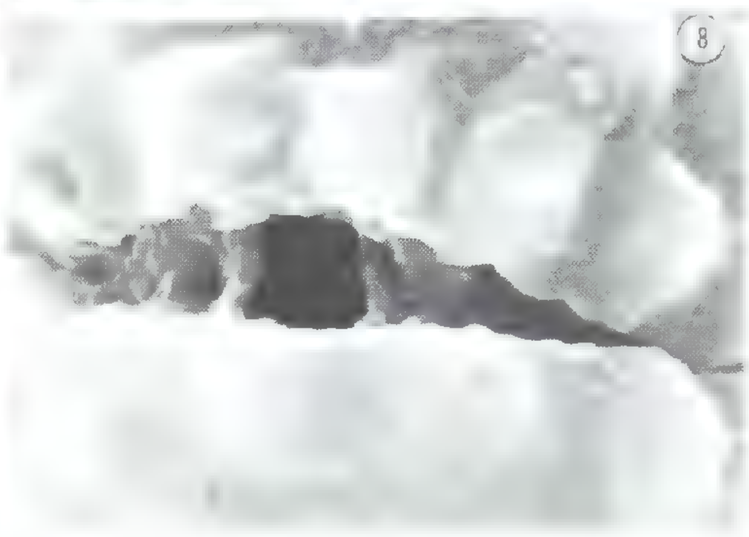
Beyond question, acetolyzed pollen provided the most clearly defined colpus-pore data. Grains were nearly always expanded and pore configurations and exine layering within the colpus were readily distinguishable (Figs. 8-9).











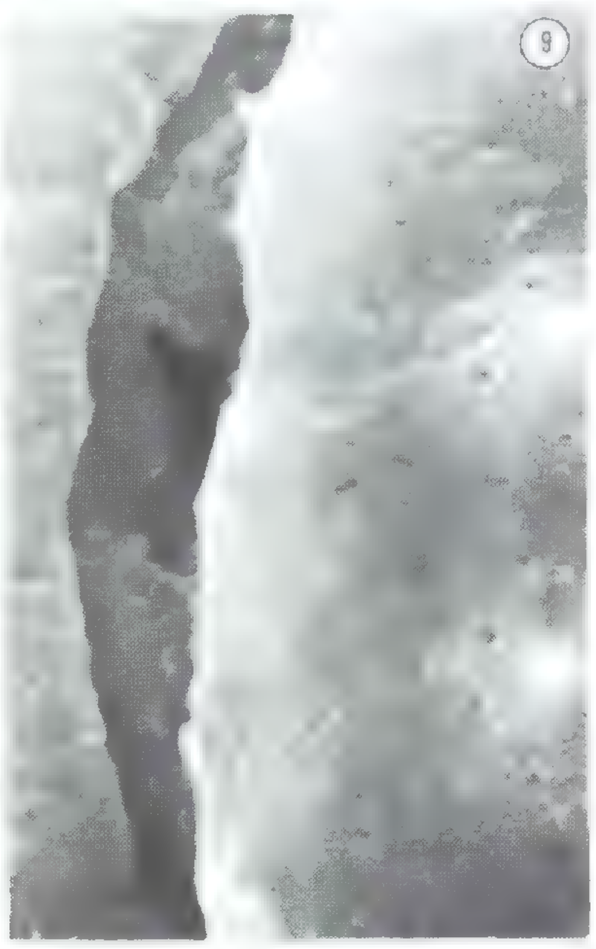


Fig. 1-9. Scanning electron micrographs of pollen. Fig. 1. Intact pore of fresh, unstained pollen of *Zea mays*, × 2900. Fig. 2. Annulus and pore of fresh, unstained pollen of *Zea mays*, × 5800. Fig. 3. Pore of fresh, OsO_4 stained pollen of *Zea mays*, × 5800. Arrows indicate endexine beneath the operculum. Fig. 4. Pore of acetolyzed pollen of *Zea mays*, × 3100. Fig. 5. Colpus and pore of fresh, unstained pollen of *Iva xanthifolia*, × 6500. Fig. 6. Same as previous figure, after contraction of colpus. Fig. 7. Fresh, unstained pollen of *Iva ciliata* showing infolding of exine at colpus, × 3300. Fig. 8. Expanded colpus of acetolyzed pollen of *Iva ciliata*, × 5400. Fig. 9. Colpus and pore of acetolyzed pollen of *Iva xanthifolia*, × 7100.

In areas away from colpi the morphology of the exine could be directly related to published work on transmission electron microscopy of thin sections (Skvarla and Larson, 1966). In such areas untreated, OsO_4-treated, and acetolyzed pollen gave similar results.

DISCUSSION

Information obtained from scanning electron microscopy of *Zea* and *Iva* pollen has indicated direct correlations with that gathered from light microscopy of whole mounts and thin sections, and electron microscopy of thin sections. These results did not in any way put a new interpretation on past analyses, but did, however, help clarify, put into a better perspective, and support these data.

Although most scanning studies have tended to emphasize the ornamentation of the pollen wall *per se,* we feel that the information presented here on germinal apertures is also of great value. Dimensions of colpi and pores can be observed easily and with greater accuracy than with light microscopy. The utilization of these parameters in taxonomic problems is obvious.

While the scanning electron microscope is designed primarily to give surface data, it is interesting to note that we have also been able to observe pollen wall stratification. It is likely that techniques will be developed which will provide more such data. That this is already nearing reality is indicated by scanning photographs of pollen which has been sectioned (Echlin, 1968).

The present study emphasizes the necessity for preparing pollen by different methods in order to gain maximum information. We have found that while fresh, untreated pollen is suitable for study, it is necessary to use fixation (OsO_4) and acetolysis for supplementation. Use of OsO_4 to stabilize labile algal and microbial specimens has provided satisfactory results (Echlin, 1968). Since procedures of OsO_4 fixation are standard in pollen studies using the transmission electron microscope, by using OsO_4 preparations in our scanning electron microscope studies, we can make direct correlative comparisons which are otherwise not possible.

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ON TROPICAL TREE SEEDLINGS[1]
I. SEEDS, SEEDLINGS, SYSTEMS, AND SYSTEMATICS

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Illustrated by Peggy K. Duke

ABSTRACT

The scattered information on characters useful in seed and seedling identification is brought together and terms defined. The problem of information retrieval in identifying seedlings is discussed and an example given of the use of a polyclave for naming an unknown. Seedling characters are given for a number of tropical families.

INTRODUCTION

For the past three years, as contractor to the Atomic Energy Commission, Battelle Memorial Institute, Columbus Laboratories, has been involved in a study of the biological feasibility of nuclear excavation of a sea-level canal in Panama or Colombia. Fiscal and temporal limitations forced emphasis on anthropological feasibility. My role, as botanist for the survey, has been to determine how man utilizes plants in the study area. Many times I have been faced with an isolated seed or fruit used by the natives. Other scientists, studying herbivore diets, may have only a seed from a fecal sample. Some of these can be identified, but usually only with difficulty. Internal morphology of the seeds provides valuable clues. Many of the seeds are still viable. Some exhibit improved germinability after passing through animals. Characters of the resulting seedlings offer more valuable clues. As seed coats often remain intimately associated with seedlings, it seems rather narrow-minded to divorce seed from seedling studies or vice versa. This introduction to the study of tropical tree seedlings presents some of the important terms and concepts.

SEEDS AND SYSTEMATICS

The importance of seeds to systematics is readily apparent in *Gray's Manual* (Fernald, 1950) where the second major division is termed "Spermatophyta" meaning seed-plants, but there are cultivated spermatophytes which bear no seeds. Subdivisions also bear titles reflecting seed characters, Gymnospermae and Angiospermae, depending on whether the carpels are open or closed, but there are exceptional angiosperms which have open carpels (*Anchietea, Butomus, Decorsella, Firmiana, Mitrasacme, Moringa, Reseda, Trillium*) (Melville, 1962). The classes, Dicotyledones and Monocotyledones, are based on the number of cotyledons but many dicots (especially in Caryophyllales and Ranales) have only one cotyledon normally developed. Some monocots, e.g., *Arisaema, Arum, Commelina, Dioscorea, Paris, Rajania, Sagittaria, Tamus, Tinantia, Trichopus,* and *Trillium,* regularly

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or aberrantly reveal traces of a second cotyledon. Some taxa are stenospermous with little seed variability, while others are euryspermous with much variability. Several *Asteraceae* and some *Rubiaceae* (with capitate inflorescences) have different types of seeds in the "ray" and "disc" flowers of the same capitulum. Species of *Stellaria* have capsules containing seeds with two types of sculpture, the percentages of each type being environmentally determined. In *Axyris amaranthoides* L., Martin (1946) reports two types of seeds from the same plant: (1) elliptic terminally alate, angular body, the surface flecked with small gray areas, (2) oval exalate, lenticular seeds with satiny dark gray body. Thus, seeds are important to systematics for the definitions of taxa, from the division to the subspecific categories.

Study of seeds will make one more sympathetic to segregation of the classic water lily assemblage into several families. Seeds of *Ceratophyllum* exhibit a rare combination of characteristics: (1) radicle not apparent, (2) plumule foliate, (3) testa spiniferous, (4) embryo investing, and (5) endosperm absent. The water lotus, *Nelumbo,* shares several fundamental characteristics with *Ceratophyllum,* such as (1) radicle not apparent, (2) plumule foliate, (3) embryo investing and endosperm absent [a correlated combination of characters rendering Martin's (1946) classification of the embryo as "broad" untenable]. An amateur readily could separate the seeds of *Nelumbo* and *Ceratophyllum* by their external morphology. *Nymphaea,* classically included in the same family with *Nelumbo,* has a radically different seed, which like its pollen, anatomy, etc., suggests monocotyledonous affinities. Definitive characters are (1) broad embryo, (2) puberulent lines, (3) white aril, and (4) copious amyloidiferous endosperm. Seed characters suggest that *Nelumbo* is closer to *Ceratophyllum* than to *Nymphaea.*

SEEDS AND RETRIEVAL SYSTEMS

Murley (1951) voiced the still-unfulfilled challenge "identification of isolated seeds is important in paleobotany, archaeology, and in the practical work of seed laboratories, for the seed is usually the only part of the plant available for identification. . . . Seed keys should be great timesavers compared to the former trial and error process." A novice confronted for the first time with water lily seeds would probably need to spend hours or even days to find out to which family the seed belonged. Toward the solution of this novice's problems, Duke (1964a, b; 1965b, c, d, e) started the polyclave, an information-retrieval system designed primarily to facilitate identification of unknowns.

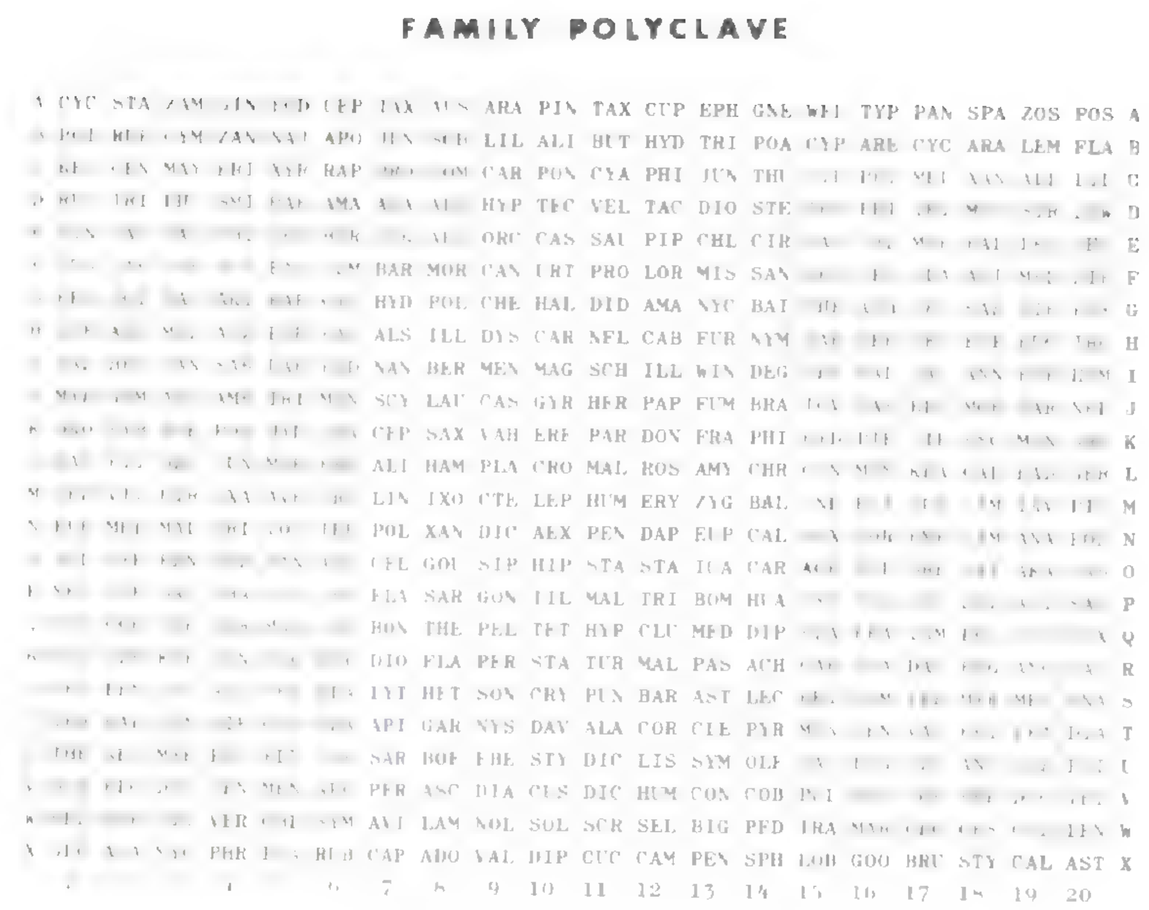
The polyclave is a coordinated index to around 800 characters, some rarely employed by seed technicians, e.g., latex, leaf type, germination type, indument, etc. Seed characters alone overcrowded the standard 5 x 8 edgepunch cards. The polyclave system recognizes 480 families arranged roughly after the Dalla Torre and Harms sequence. Abbreviations of these 480 families are shown in the Family Polyclave Underlay (Plate 1). Plate 1 also contains underlays for Missouri, Panama, and Viet Nam, with abbreviations of the families reported in their respective floras. These underlays, or positives, are printed in color, with plus signs in each corner. Plate 2 shows various character overlay cards or negatives updated

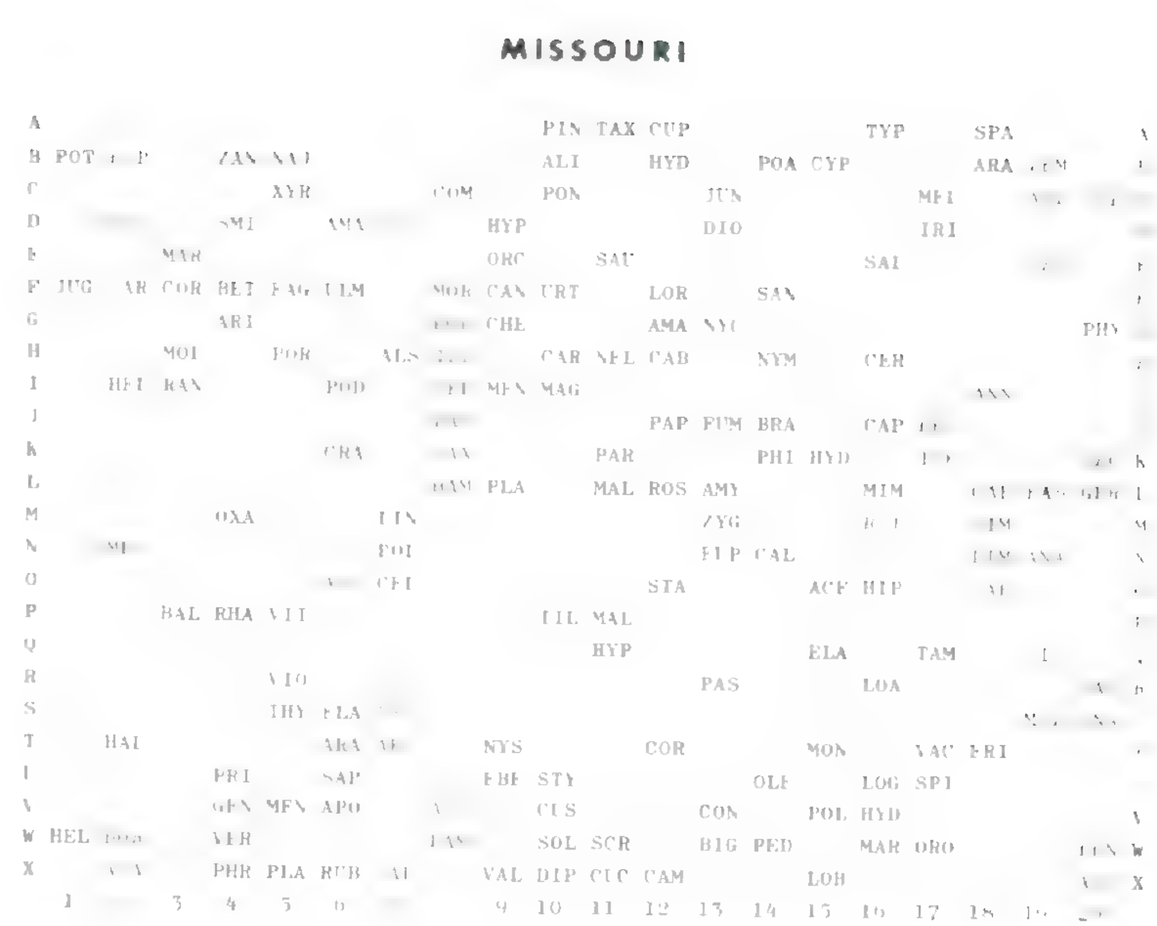
since publication of the polyclave. Negatives are printed in black and white or black and transparent and bear a minus (—) sign in each corner. Blanks in the overlays represent families recorded to have the characters. Acetate transparencies of these cards can be superimposed over the corresponding underlay or positive. Then only the abbreviations which show through in color correspond to families possessing the characters.

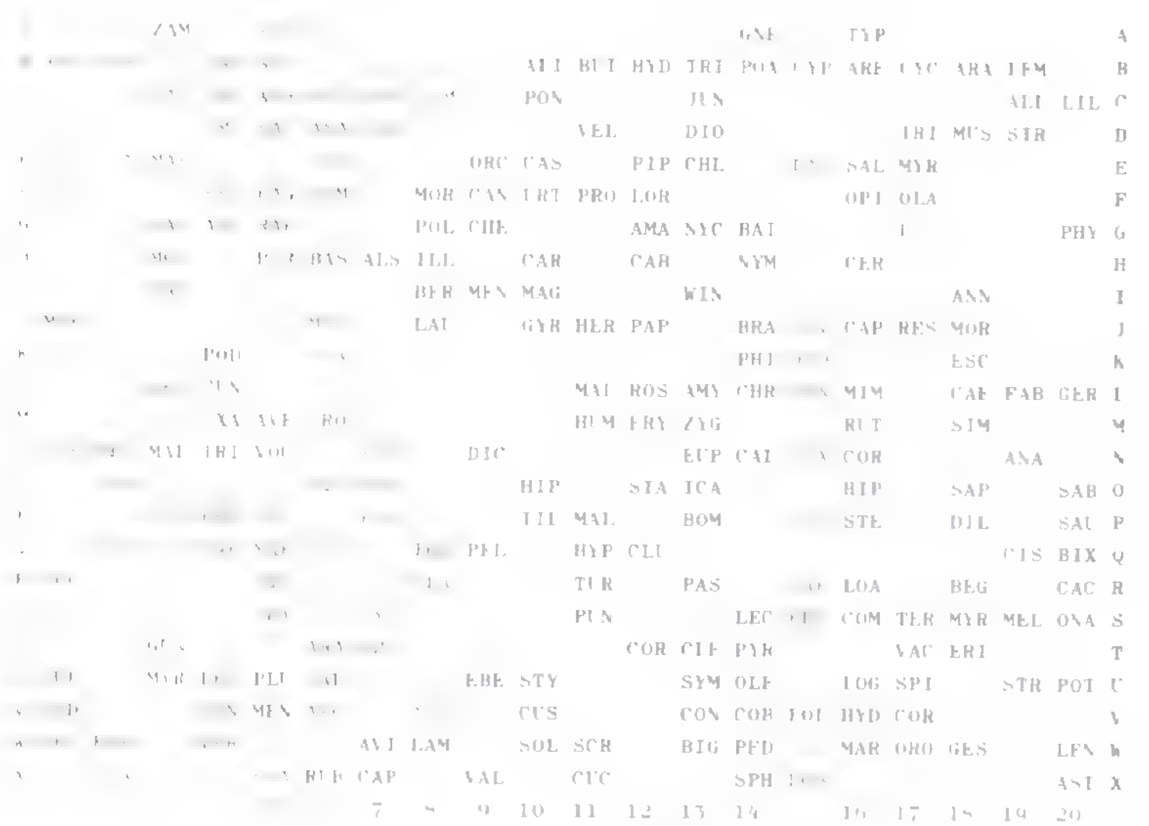
Seeds of the water lily allies afford good examples of the polyclave approach, but some poisonous fabaceous seeds afford a more colorful demonstration. In Plate 2, abbreviations of families reported to have red seeds have been erased. Superpose the corresponding transparency over the family underlay and you read in color abbreviations of those families reported to have red seeds. Similarly, superpose the transparency for black seeds over an underlay and you read in color only those families reported to have black seeds. Superpose both transparencies over the underlay and you read in color only those families reported to have both characters. Add to these the transparency for poisonous seeds, and you see in color only the few families reported to have the three characters. Refer to Figure 23 and note that the seedlings of *Ormosia* have stipels, a rare character reported only in those families whose abbreviations have been removed from the transparency for stipellate eophylls. Superpose all four transparencies and you will read in color "FAB," for *Fabaceae,* to which *Ormosia* belongs. With four transparencies, most families have been eliminated from consideration. In the polyclave (Duke 1969b) there are 770 character negatives scored for various taxonomic characters, about half of which are useful in determining the family of unknown seeds and seedlings. Superposition of any combination of these eliminates families not reported to have the characters. Theoretically, if an unknown has nine uncorrelated characters, each of which occurs in only half of the 480 families, superposition of the nine corresponding character transparencies would eliminate all but one family. Because of parallel evolution and flaws in existing classifications, however, several families may turn up, although perhaps few or no species in each may have the combination of nine characters. A retrieval system at the generic level would be more efficient, but it would be a sizeable chore to score some 20,000 genera, many with over a hundred species each, for a thousand characters. Beginnings have been made for the genera of grasses (Duke, Gunn, and Terrell, unpublished), legumes (Duke, 1965e, 1969), and palms (Duke, 1965d).

Seeds

OVULES Seeds, like other plant entities, defy rigid definition, but a common definition is "fertilized ovule." The angiosperm ovule consists of a central body, enclosed more or less completely by one or two integuments and supported on a basal stalk, the *funicle.* The central body consists of the *nucellus,* a distal part, in which sporogenous tissue is borne, and the *chalaza,* a basal part where funicle, integuments, and nucellus merge. In sessile ovules, the funicle is absent, but in some the funicle may be elongate and adnate to the ovule body forming a ridge, the *raphe.* The scar on mature seeds known as the *hilum* represents the point of attachment of the funicle (or carpel wall in sessile ovules). Generally there are one or two integu-







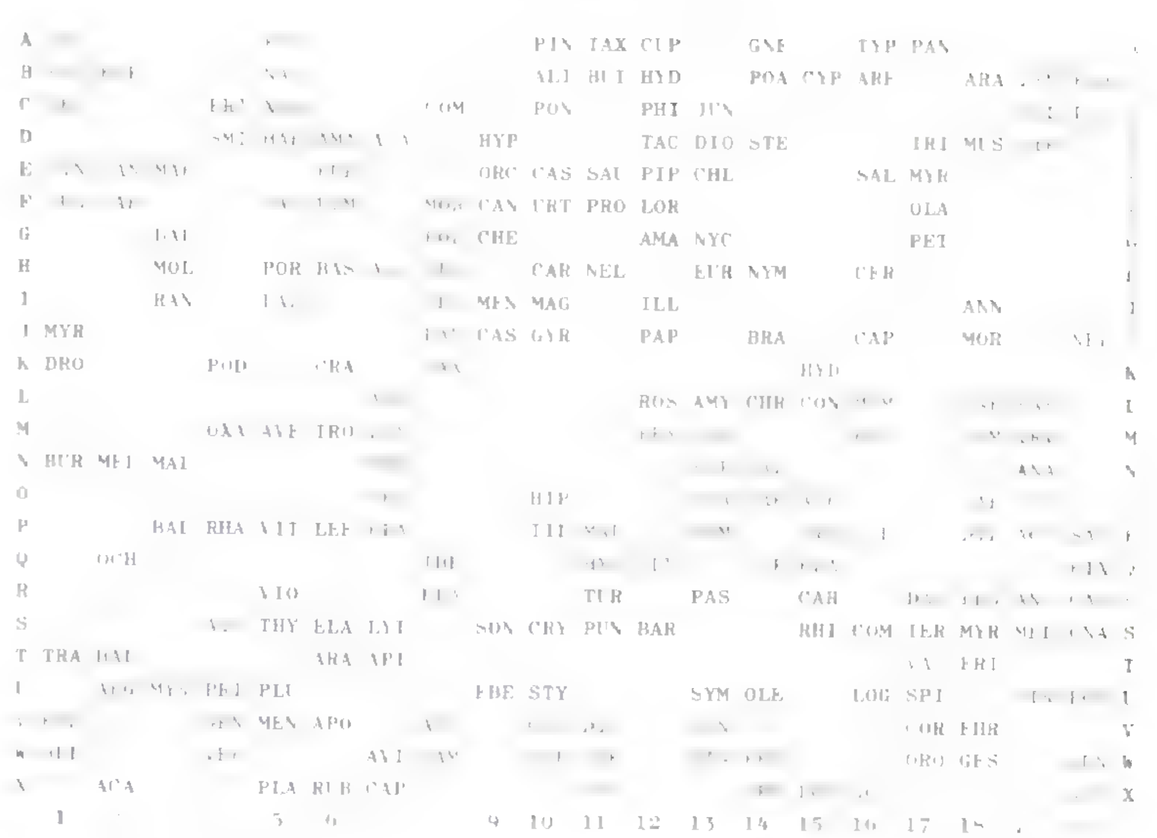
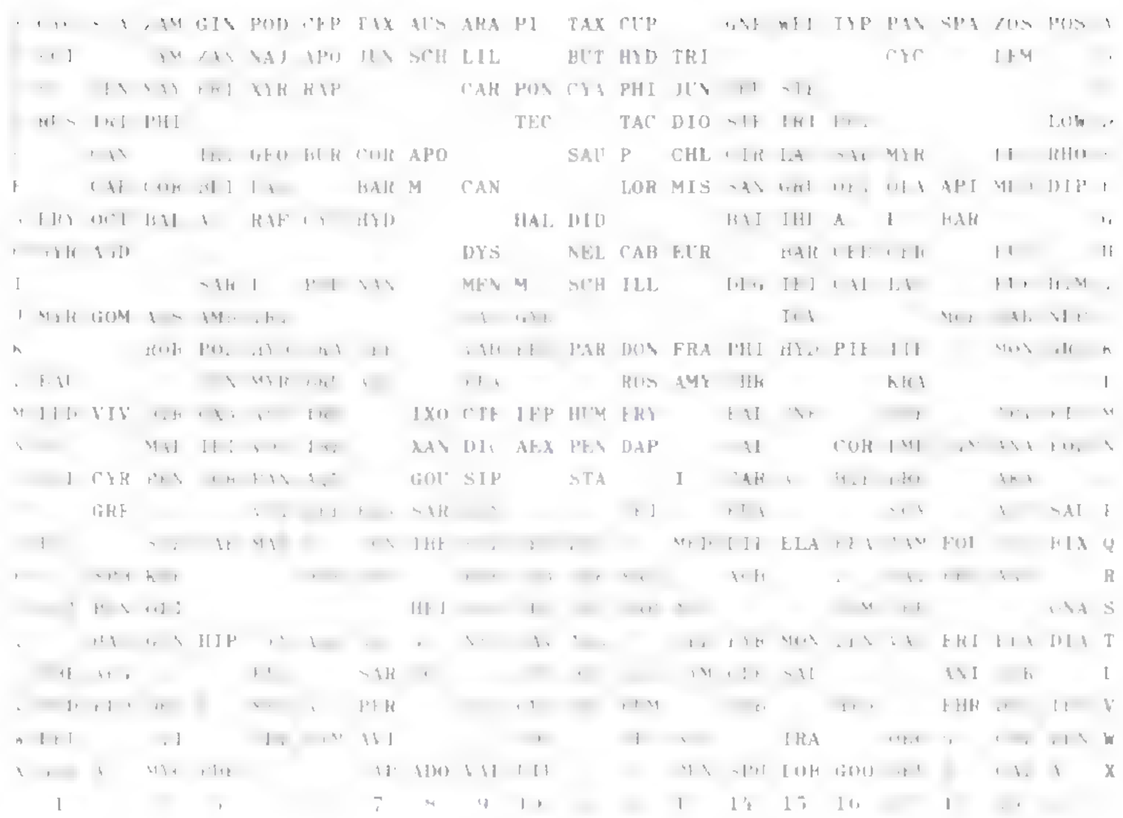
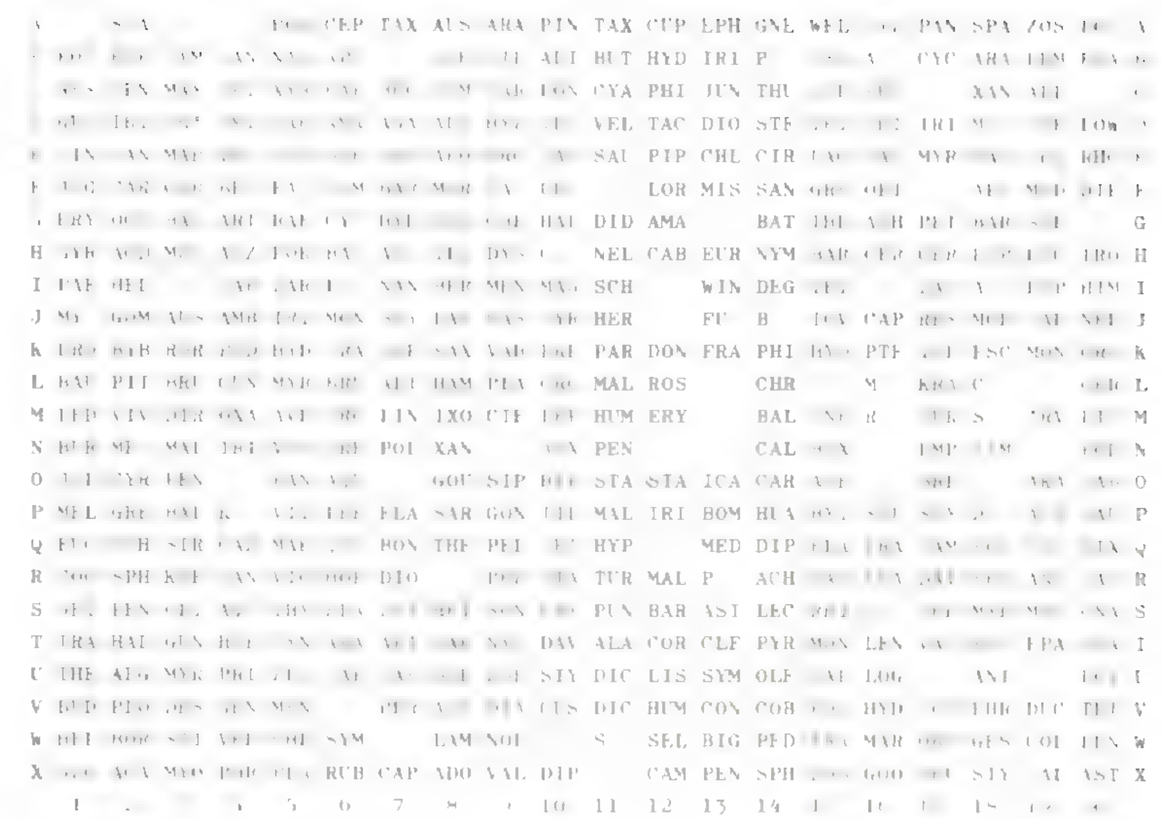


Plate 1. Underlays from the family polyclave.





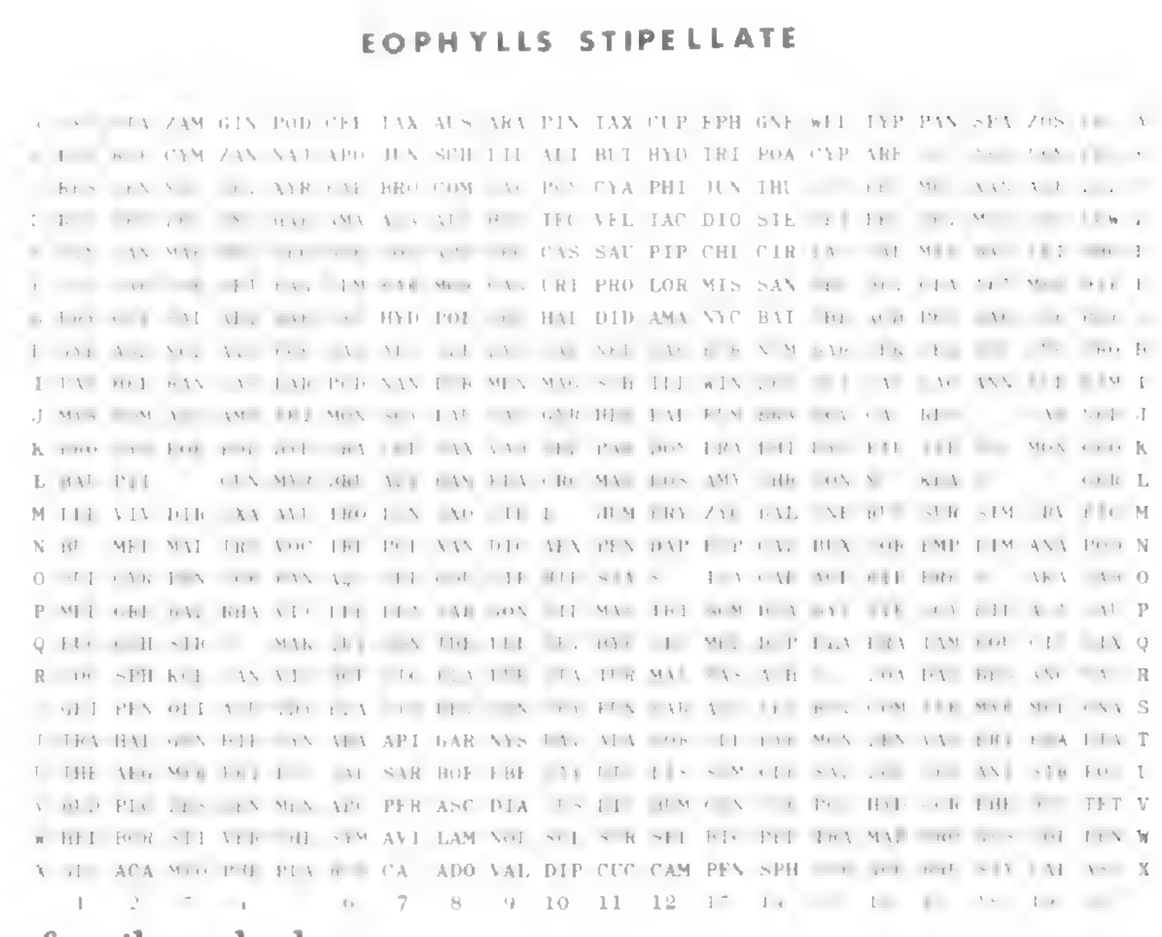


Plate 2. Overlays from the family polyclave.

ments, more or less fused to each other and to the central body, but in specialized ategmic types the integuments are absent, e.g., some Balanophorales and Santalales. The opening between the tips of the integuments where the nucellus is exposed is termed the *micropyle*. *Arils*, loosely defined as investing outgrowths from the chalazal region, have been questionably interpreted as third integuments and as primitive. Freedom of the nucellus from the integuments as in *Amphipterygium*, *Cananga*, *Casuarina*, *Cleome*, *Juglans*, and *Myrica* seems rare. Freedom of the two integuments occurs in some Amentiferae, *Capparaceae*, *Fabaceae*, *Ranunculaceae*, and *Rosaceae*. Where there are two, the outer usually is more massive and longer than the inner. Occasionally in the *Annonaceae*, *Cactaceae*, *Proteaceae*, and *Trapaceae*, the inner projects beyond the outer. Bitegmic anatropous ovules usually have only one integument obvious on the side adjacent to the funicle. Number of integuments is not a constant indicator of relationships. Most species of *Populus* have two integuments, but two species and all *Salix* species known, have only one (Eames, 1961). *Peperomia* has one integument, while other *Piperaceae* have two. Both integuments are absent in some *Olacaceae* and *Opiliaceae*. As a rule, gamopetalous dicots are unitegmic but *Primulaceae* and *Cucurbitaceae* are bitegmic.

OVULAR TYPES Ovules are termed *crassinucellar* when the nucellus is massive and the megaspore mother cells are deep in the distal tissue and *tenuinucellar* when the nucellus is small and delicate and the spore mother cells (usually one) are directly below the epidermis. The two types intergrade. Crassinucellar is more primitive, usually accompanied by two integuments. The ovule is *orthotropous* (loosely synonymous with *atropous*) when straight and upright on the placental surface, with the micropyle distal and the funicle short or absent. It is *anatropous* when bent upon itself and more or less adnate to the funicle, with the micropyle facing the placenta. Cronquist (1968) states that the anatropous condition is eventually derived from the orthotropous. It is *campylotropous* when the ovule is reniform, attached near the middle, and the micropyle faces the placenta. It is *amphitropous* when the funicle is adnate to the ovule for about half its length and the micropyle faces laterally. Anatropy is more common and characterizes many primitive taxa (e.g., in Ranales, Helobiae, *Nymphaeaceae*). Orthotropy occurs in more specialized groups with solitary ovules and basal placentation — *Juglandaceae*, *Najadaceae*, *Piperaceae*, *Polygonaceae*, and *Restionaceae*. Campylotropy characterizes *Apocynaceae*, *Capparaceae*, *Caryophyllaceae*, *Geraniaceae*, and *Verbenaceae*. Orthotropy, though superficially more simple, seems to be derived as in the Urticales. *Ulmaceae* and *Moraceae* have suspended anatropous ovules, *Laportea* is transitional and *Urtica* and *Boehmeria* have basal orthotropous ovules. *Circinotropous* or coiled ovules are rare but occur in *Cactaceae*.

STOMATAL TYPES The outer integument has normal stomata (Eames, 1961), and in some cases, stomatal types may serve as indicators:

Actinocytic: Stoma encircled by a rosette of subsidiary cells.

Anisocytic ("cruciferous"): Stoma surrounded by three cells of which one is distinctly smaller than the other two.

Anomocytic ("ranunculaceous"): Stoma surrounded by a limited number of cells that are indistinguishable in size, shape, or form from those of the remainder of the epidermis. (Type 4; Stebbins and Khush, 1961.)

Diacytic ("caryophyllaceous"): Stoma enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells.

Didymocytic ("arecaceous"): Stoma enclosed by four subsidiary cells, the pairs dissimilar. (Type 2; Stebbins and Khush, 1961.)

"Gramineous": Guard cells with the middle portions much narrower than the ends giving a dumbbell appearance in surface view. Stomata tend to disappear as the seed matures, but they are reported in *Canna indica, Carpolyza spiralis,* and *Nerine bowdeni* (Boyd, 1932).

Paracytic ("rubiaceous"): Stoma accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells. (Types 1 and 3; Stebbins and Khush, 1961.)

Triacytic ("gordoniaceous"): Guard cells with three subsidiaries similar to each other, but differentiated from the epidermis.

ENDOSPERM The so-called double fertilization results in two chains of events, the one leading to embryo formation, the other to endosperm formation. In all monocots and dicots so far investigated (Swamy and Ganapathy, 1957) endosperm formation follows one of three sequences in development.

Nuclear: Initial division and usually subsequent ones are not followed by wall deposition. Nuclei may remain free or later be separated by walls.

Cellular: First and several subsequent divisions accompanied by wall formation.

Helobial: A transverse wall is laid down following the initial division, dividing the embryo sac into a micropylar and a chalazal chamber. Subsequent divisions are generally free-nuclear and may take place in both chambers, but invariably the main bulk of the endosperm is formed by the micropylar chamber.

These developmental types will be of little use in identification of unknowns, but may be correlated with other characteristics. Sporne (1954), working on external morphological correlates concluded that the nuclear type was primitive, while Swamy and Ganapathy (1957), correlating with wood anatomy, concluded that the cellular type was less advanced. Cronquist (1968) notes that in the *Gentianaceae,* characterized by nuclear endosperm, two advanced mycotrophs, *Voyria* and *Voryriella,* have cellular endosperm. Presence or absence of endosperm is a useful character. Ruminations in the endosperm are frequently diagnostic, and may arise (1) through expansion of the developing endosperm into furrows in the integument or (2) through invagination into the endosperm of peripheral tissues. The latter may explain the peculiar tendency to cryptocotylar germination in some *Annonaceae.*

The chemical and physical nature of the endosperm is occasionally diagnostic. Dissection in water of many seeds characterized by oily endosperm will yield an

obvious oil-slick. The IKI starch test can be used to detect amyloidiferous endosperm in embryos. *Simmondsia chinensis* is unique among plants in that its seed oil is not a fat but a liquid wax.

Endosperm may be absorbed by the embryo before (exalbuminous seeds) or after germination (albuminous seeds). Cronquist (1968) notes that the absorption may take place rather late in ontogeny, as in many of the *Sapotaceae,* in which the endosperm is obvious in young seeds but wanting or scanty in mature seeds. In some germinating seeds, the endosperm is raised characteristically above the ground with or without the testa. In members of the Myrtales and many aquatics, the hypocotyl is the storage region, greatly swollen at the expense of the cotyledons to form the type of embryo termed *macropodial. Perisperm,* nutritive tissue derived from the nucellus or integuments, may be present in addition to endosperm, and is associated with the "peripheral" embryos of Martin (1946). Cronquist (1968) states that perisperm is clearly an advanced condition. During germination, the food is absorbed from the perisperm by the endosperm and thence is passed on to the embryo.

SEED SIZE AND SHAPE As Eames (1961) notes, both large and small seeds have been considered primitive. Large seed size has quite naturally been correlated with the tree habit, and therefore deemed primitive. For examples of variation in the families, witness the palms, with huge seeds like *Cocos* and small ones like *Prestoea,* and the legumes, with small seeds like *Trifolium* and large seeds like *Mora.* Nonetheless, the novice faced with an unknown could eliminate much work if he knew what groups had the same size seeds as the unknown.

The same is true of seed shapes. Who knows which shapes are most frequent — ellipsoid, reniform, lenticular, globose, ovoid, oblong, or segmentoid? Among the myriad of other shapes possible, some are quite rare, and the knowledge of which families exhibit which types can save an immense amount of random searching.

TESTA As the seed develops from the fertilized ovule, the integuments develop the seed coat or testa. Both integuments may still be recognizable in some *Euphorbiaceae, Rosaceae,* and *Rutaceae,* but more commonly the inner is lost or drastically reduced. In others, such as *Opiliaceae and Pelliceriaceae,* there is no testa. Appendages are quite often useful clues to affinities. Most important are *wings, arils* [fleshy transformations of the outer layers of the outer integument (=sarcotestae), of the chalaza or of the distal part of the funicle], *arilloids* (those developing from the micropylar rim of the integuments), *strophioles* (fleshy tissues restricted to crests, as along the raphe), *caruncles* (restricted to the base or apex of the seed), *glochidiae, spines, tubercles,* and various types of *hairs,* which may be more or less restricted to the dorsal surface of the seeds as in some *Bombacaceae, Malvaceae, Convolvulaceae,* and *Caryophyllaceae* or concentrated in *comas* at one end of the seed, as in some *Onagraceae, Apocynaceae,* and *Asclepiadaceae.* Specialized appendages, much resembling modifications of the caruncle, are cap-like *operculi* (e.g., in *Commelinaceae*) which seem to facilitate

emergence of the seedling, and *coronae* (apical annular crowns as occur in certain *Boraginaceae* and *Euphorbiaceae*). Several seeds exhibit combinations of the above characteristics, and several of the above characteristics intergrade. Corner (1954) suggests that the truly arillate seed is primitive in angiosperms, but arils and sarcotestae are generally regarded as adaptations for seed dispersal. Alate and comose seeds are clearly derived adaptations when compared to seeds with no special dispersal mechanisms.

Less prominent markings of the testa have been treated in detail by Murley (1951), and an elaborate terminology has been erected and illustrated. Brown probably is the most frequent seed color, with other colors occurring in less than half the families. Particular types of seeds, often seen in necklaces, are *ocellate* and *halonate* seeds, which are frequent in legumes. Ocellate seeds have a large spot of color, like an eyeball, such as the black-eyed red seeds of *Abrus, Ormosia,* etc. Halonate seeds have a circle of lighter or darker color prominent in the seed as in *Enterolobium cyclocarpum* (Duke, 1965a).

CHEMISTRY Earle and Jones (1962) published results of chemical analyses of seed samples from 113 plant families and their research continues to expand the number of families, genera, and species investigated. Valuable biochemical data presented at a specific level are percent ash, protein, and oil; weight per 1000 seeds; fraction of alcohol-soluble nitrogen; fraction of trichloracetic-acid-soluble nitrogen, reactions of starch test, alkaloid test, tannin test, etc.

UTILITY AND GEOGRAPHY Most botanists at several points in their career will have received seeds for identification with no other information than: "This seed is used by the natives (1) to poison fish, (2) to eat raw, (3) to make necklaces, (4) to poison animals, (5) as an anthelmintic, (6) as an oil source, (7) pulverized as an insecticide, (8) as a starch source, (9) as a candle, etc." Or the letter may read, "The enclosed seed was found: (1) germinating in sea drift, (2) among the belongings of a jazz musician, (3) to constitute 90% of the tufted titmouse's food intake, (4) clinging to the clothing of an exile Cuban, (5) in a Navajo campsite, (6) mixed in with pollen 1000 feet above New York City, (7) to cause dermatitis among three prisoners, (8) in the ejecta of a regurgitating child, (9) as a frequent fossil in a Pleistocene deposit, etc."

Unsolicited letters arrive by the hundreds in botanical gardens all over the world with statements like the above followed by the question "What is it?" Responsible taxonomists faced with such queries have spent days combing the literature to find out which seeds are barbascos, poisonous, edible, common in sea drift, airborne, allergenic, ornamental, etc. It is sad that most of their hand-scribbled notes could not be transcribed to an information retrieval system available to subsequent botanists.

Knowledge of the origin of the seed can be equally useful if entered into the system. There are many genera with brilliant red seeds, but how many occur in your backyard, in your state, in your country, in your continent, in your hemisphere?

EMBRYO

PROEMBRYO The following key serves to distinguish the main types of proembryo:

I. Division of zygote longitudinal . . . . . Piperad type

II. Division of zygote transverse:

A. Division in terminal cell transverse:

1. Basal cell plays essential part in development of the embryo proper . . . . . Chenopodiad type

2. Basal cell plays no essential part in development of the embryo proper:

(a) Basal cell divides no further and becomes a large suspensor cell (suspensors of a few cells, but derived from the terminal cell, may be present) . . . . . Caryophyllad type

(b) Basal cell usually forms a suspensor of two or more cells . . . . . Solanad type

B. Division in terminal cell longitudinal:

1. Both basal and terminal cells take part in further development of embryo . . . . . Asterad type

2. Basal cell plays little or no part in development of the embryo . . . . . Onagrad type ("crucifer type")

Further information on embryology will be found in Davis (1966).

EMBRYO Martin (1946) recognized 12 embryo types among seed plants. Some categories overlap with others, but this in no way destroys their taxonomic usefulness. Some of his categories are broad and are subdivided in the polyclave.

A. *Basal* (Embryo at One Pole of Seed)

1. *Rudimentary:* Small, nonperipheral embryo in medium to large seed, more than 2 mm long, the endosperm copious but rarely starchy. Martin has taken this type as the progenitor of the other types in a novel phylogenetic scheme based on embryo types. It roughly groups the Centrospermae on a limb equivalent to the monocot and dicot limbs. Large seeds with small embryo and copious endosperm are rather characteristic of both the woody and herbaceous Ranales and are frequent in the *Liliaceae-Amaryllidaceae* alliance as well as in palms and sedges. Intergrading with the rudimentary are two small categories, the Broad and the Capitate.

2. *Broad:* A globular or lenticular embryo in copious starchy endosperm. Martin lists few examples of the broad embryo. *Nelumbonaceae,* which has anything but a broad embryo as defined by Martin, should be classified as investing. Broad embryos occur infrequently in aquatic or palustrine, more or less primitive dicots and monocots, and in a few parasites.

3. *Capitate:* A capitate or turbinate, more or less basal, embryo in copious starchy endosperm. Closely related to the broad embryo, this type occurs in about ten families. Capitate and broad embryos seem to be correlated with operculate seeds.
4. *Lateral:* Although characteristic of more genera than the preceding, the lateral embryo is characteristic of fewer families, one of them being the grasses. Reeder (1957) illustrates the usefulness of the embryo in grass systematics. Embryos of *Cynomoriaceae, Bromeliaceae,* and *Centrolepidaceae* could be included according to the definition "embryo basal-lateral or lateral and evident from the exterior, usually with copious starchy endosperm." The lateral subdivision, found only in monocots, except for apparent occurrence in *Cynomoriaceae,* indicates a transition to the Peripheral division.

B. *Peripheral*

Embryo ordinarily elongate and large, quarter to dominant, contiguous in part, at least to the testa; perisperm starchy, central or rarely lateral; cotyledons narrow or expanded; dicots with one cotyledon occasionally abortive. This roughly coincides with the Centrospermae but other taxa approach the peripheral condition, e.g., members of *Cactaceae, Cuscutaceae, Frankeniaceae, Ulmaceae,* etc. (To further suggest the resemblance of Centrospermae to monocots, consider also the farinose starchy endosperm, characteristic of the Farinosae of monocots, and the tendency toward geniculate, ensheathed nodes.) In the peripheral division are straight, arcuate, hippocrepiform, annular, and spirolobal embryos. Many dicot peripheral embryos have the second cotyledon reduced (anisocotylar, as in *Wittia,* Fig. 60) or absent. Peculiarities shared by many families with peripheral embryos are possession of beta-cyanin and polyporate pollen grains. Polyporate pollen grains also occur in *Alismataceae* where, e.g., *Sagittaria* has rudiments of a second cotyledon.

C. *Axile*

1. Linear Subdivision:
   (a) *Linear:* Embryo axial, generally several times longer than broad, straight, curved or coiled; cotyledons not expanded; seeds normally not minute; endosperm not starchy (rarely so in monocots). Martin notes a distinct group, *Cannaceae, Marantaceae, Pontederiaceae, Sparganiaceae,* and *Zosteraceae,* which are unique among linear seeds in having starchy endosperm and in having the base of the embryo extend into a depression at one end of the seed, as in some *Commelinaceae,* and *Arecaceae,* in *Caulophyllum thalictroides (Podophyllaceae),* and perhaps in *Loranthaceae.* The linear division is well represented in gymnosperms, monocots, and dicots. Included are straight, arcuate, hippocrepiform, annular, and spirolobal embryos with or without endosperm. These could be separated from their peripheral counterparts only by the excentric endosperm which

supposedly would not give a starch test when present. Many aquatic monocots absorb all the reserves into a "foot." Macropodial embryos occur, e.g., in *Alismataceae, Clusiaceae, Hydrocharitaceae, Lecythidaceae, Welwitschiaceae, Zosteraceae,* etc.

(b) *Dwarf:* Embryo variable in relative size, small to total, generally stocky, cotyledons often poorly developed; seeds exclusive of testa mostly 0.3-2.0 mm long, often nearly as broad as long. This type occurs in many sympetalous families, e.g., *Ericaceae, Gentianaceae, Loganiaceae, Scrophulariaceae,* and *Solanaceae.* Parasitic derivatives of these are more likely to have the following:

(c) *Micro:* Seeds usually minute, less than 0.2 mm long, exclusive of testa, few-celled (50 to 150); embryo undifferentiated to total.

2. Foliate Subdivision:

(a) *Spatulate:* Embryo erect; cotyledons variable, thin to thick and slightly expanded to broad. The spatulate type occurs in more families than any other, closely rivaled by the linear (Martin, 1946). Since these are most common, they are least valuable for purposes of identifying unknowns. It would be practical to divide the spatulate into subclasses based on cotyledon shape and relative lengths of hypocotyl and cotyledon (the H:C ratio in the polyclave).

(b) *Bent:* With expanded cotyledons in an axile position but with the cotyledons bent upon the hypocotyl in a jackknife fashion; cotyledons are generally thick or planoconvex but not necessarily so. In the commonest type, the bend is in the plane of the cotyledons, i.e., accumbent *(pleurorhizal)* (o =). The bend may be contra the cotyledonary plane, i.e., incumbent *(notorhizal)* (o ||). The *oblique* embryo is intermediate between accumbent and incumbent (o //). The term oblique is unfortunate since certain "linear" embryos are oriented obliquely to the long axis of the seed, e.g., *Clintonia.* In a fourth type *(orthoplocal),* the cotyledons in addition to being incumbent, are conduplicate (o >>). Such an embryo occurs in *Avicennia.* Martin would probably have classified this as a "folded" embryo. Spirolobal embryos have incumbent cotyledons, once folded (o || ||) while diplecolobal embryos have two or more folds (o || || ||). All these "bent" embryos occur within the *Brassicaceae* and sporadically in other families. Rare convolute cotyledons occur in *Terminalia.*

(c) *Folded:* "Embryo with cotyledons usually thin, extensively expanded and folded in various ways." Many of the embryos diagrammed by Martin could be called incumbent or diplecolobal. Weirdly folded or *contortuplicate* cotyledons are frequent in the Sapindales and Malvales. The *Convolvulaceae,* also characterized by folded cotyledons, frequently share with the *Malvaceae* and *Myrtaceae* the characteristic of punctate cotyledons.

(d) *Investing:* The last of Martin's categories is defined under his AXILE division: "Embryo erect and with thick cotyledons overlapping and encasing the somewhat dwarfed stalk for at least half its length; endosperm wanting or limited." This would merge at the halfway point with both the folded and the spatulate types. Species having both foliate plumules and straight embryos would usually fit this category. Investing embryos are not common, but frequently are associated with cryptocotylar germination.

Polyembryony

Polyembryony, the presence of more than one embryo in an ovule or seed, is not uncommon, and is characteristic of some groups. Secondary embryos may be adventive, arising from mother sporophytic tissue, or may derive from cleavage of the daughter sporophyte (embryo), or they may be haploid and derived from gametophytic nuclei other than the egg. Adventive embryos of nucellar origin are more common than those of integumentary origin, and have been said to exist in 19 percent of *Trillium undulatum* ovules. *Citrus, Eugenia,* and *Mangifera* are tropical genera notorious for polyembryony.

Dormancy and Vivipary

Some seed technologists avoid the use of internal morphology and the seedling. Many small seeds germinate rapidly without scarification and the seedling yields additional characters for determination of an unknown. Faced with seeds brought to me for identification in Panama, I planted the seeds and ten days later had seedlings of *Cannabis* (Fig. 10), thereby confirming my suspicions. Some seeds are germinating before they are shed. In *Cycadaceae* and *Ginkgoaceae,* there may be no embryo when the "seed" is shed, but in most if not all angiosperms, the embryo is present in some stage of development, frequently continuing its development after shedding. Some seem to have no dormant period, e.g., *Annona, Durio, Myristica,* and *Thalassia.* Eames (1961) suggests that dormancy represents an advanced stage in the evolution of the seed. After-ripening—morphological and physiological—may delay readiness to germinate until long after shedding. Eames states that size of seed seems less important, from the standpoint of primitiveness, than time of inception of dormancy and stage of specialization of the embryo. Since primitive gymnosperms and a few angiosperms lack dormancy, and since there is a long-continuing, after-ripening process in some primitive families, absence of dormancy seems primitive. Duke (in press) finds larger seeds and quicker germination in species of the rain forest than in drier forest types.

Examples reported by Eames (1961) of time necessary to complete growth from seed-shedding stage to germinating stage are *Fumaria,* 8 days; *Caltha,* 10 days; *Clematis,* 17 days; *Actaea, Hepatica,* and *Thalictrum,* 2 months; *Cocos, Fraxinus,* and *Paris,* 4 months; *Crocus,* 6 months; *Corydalis,* 10 months; *Trillium,* 12 months. Data presented by Marrero (1949) for tropical tree species, suggest that cryptocotylar species (22) average 41 days between sowing and germination while phanerocotylar species (35) average 23 days.

Vivipary, an obvious example of lack of dormancy, has been attributed to some tropical tree species, especially mangroves. Seeds not truly viviparous, e.g., *Capparis, Hura,* and *Inga* (Fig. 17), have been reported as germinating before falling from the tree, but such cases are probably due to unusual meteorological conditions rather than inherent characteristics of the species. Often, seedlings will be found intimately associated with fruits on the forest floor. On account of such an association, the author was able to identify the seedlings of *Apeiba, Clusia,* and *Enallagma,* all with many-seeded fruits, sometimes important in mammal diets. The flattened subspherical tuberculate fruits of *Apeiba,* the 5-locular superior fruits of *Clusia,* and the large globose fruits of *Enallagma* offer combinations of characters occurring in few families. The combination of operculate fruits with palmilobed cotyledons that characterizes *Cariniana* (Fig. 66) apparently occurs only in the *Lecythidaceae*. Coupling fruit characters with those of the seeds and seedlings renders determinations more certain.

A second dormancy occurs in many tropical seedlings, in the dipterocarps in Asia and, e.g., in *Connarus* (Fig. 16) and *Ormosia* (Fig. 23) in Panama. Such species go into a state of dormancy after the cotyledons and first eophylls are raised and fully expanded, awaiting some ecological trigger to further their development.

Seedlings

GERMINATION There are two types of germination, *phanerocotylar,* in which the cotyledons emerge from the seed, and *cryptocotylar,* in which the cotyledons do not emerge from the seed (Duke, 1965a). Phanerocotyly is more common in dicotyledons, cryptocotyly in monocots. The peanut is a transitional type, while many genera have species with both types, e.g., *Acer, Bauhinia, Caesalpinia, Clematis, Couratari, Lecythis, Ormosia, Passiflora, Phaseolus, Pithecellobium, Prunus, Pterocarpus, Quercus, Rhamnus, Rubia, Sapindus, Sophora, Sterculia, Terminalia, Theobroma,* and *Trichosanthes.* Eames (1961) states that the hypogeal (cryptocotylar) method is clearly advanced. However, in *Phaseolus,* cryptocotyly is a Mendelian dominant to phanerocotyly (Compton, 1912). Among cryptocotylar dicots, two types seem rather rare and definitive: those in which scale leaves (cataphylls) preceding the foliage leaves are opposite *(Bignoniaceae, Clusiaceae, Melastomaceae).* The common type has small spiral or alternate cataphylls preceding the foliage leaves as in *Gustavia* (Fig. 65). *Annonaceae, Hura,* and several *Rubiaceae,* e.g., *Pentagonia* (Fig. 77) and *Tocoyena* (Fig. 79) exhibit a peculiar transitional condition. The cotyledons tardily emerge from the seeds, or may break off in the seed, unless man or accident breaks the seed coat. Usually the radicle is the first structure to emerge from the seed, but rarely the plumule emerges first.

The hypocotyl is the portion of the axis where the stem-root transition occurs. Occasionally there is an external demarcation, the *collet,* between hypocotyl and root. The cryptocotylar forms are often described as being devoid of hypocotyl, but the transition must occur. Compton (1912) has differentiated three types of transition in the legumes. The *epicotyl,* the embryonic axis above the cotyledonary

node, is often not obvious in the seed until after germination, but it tends to be better developed in cryptocotylar species before germination.

SEEDLING AXIS After germination, the distinction between hypocotyl and epicotyl is more easily made (cf. *Virola,* Fig. 12). Frequently the hypocotyl will be swollen, pegged, or annulate near the soil. In many woody species such as *Tamarindus* and *Virola* (Fig. 12) the epicotyl and hypocotyl have different indu-ments and textures. In species destined to become stilted or buttressed, such as *Cecropia peltata* and *Sloanea herteriana,* adventitious roots are often obvious at the seedling stage (Duke, 1965a). Swollen hypocotyls are not uncommon in species destined to have swollen trunks.

In Puerto Rican tree seedlings studies (Duke, 1965a), all laticiferous species except *Pterocarpus* had obvious latex by the first eophyll stage. In the seedling stage, *Bursera* and *Dacryodes* already exhibit the characteristic aroma of turpen-tine; seedlings of many *Lauraceae* and *Myrtaceae,* e.g., *Pimenta,* may be dis-tinguished by their odors; seedlings of *Cedrela odorata* and *Cordia alliodora* are said to possess the characteristic alliaceous odor. A notebook containing a seedling of *Quararibea* smells about as pleasant as a herbarium case containing dried specimens. Spines may be evident quite early (second eophyll stage in *Acacia farnesiana*) (Duke, 1965a) and tardily develop in the axils of the cotyledons of *Pereskia bleo.*

Bailey's survey (1956) of 99 dicot families showed that 77 percent of the seedlings have an even number of strands at the cotyledonary node, and 60 percent of the cotyledons have two independent traces related to a single gap. The double-trace, unilacunar node is not confined to a few genera, but is of common occurrence in many orders of dicotyledons. This contrasts markedly with the foliar nodes, where the majority of dicots have an odd number of traces. The double-trace unilacunar node has been reported for foliar nodes only in certain *Am-borellaceae, Austrobaileyaceae, Calycanthaceae, Chloranthaceae, Hernandiaceae, Lamiaceae, Lactoridaceae, Lauraceae, Solanaceae, Trimeniaceae,* and *Verbenaceae.* Bailey observed no cotyledons with multilacunar attachments, but pentalacunar attachments are reported for *Fitchia speciosa (Asteraceae)* and multilacunar for *Gustavia (Lecythidaceae)* (Carlquist, 1961).

If the trilacunar condition is primitive, and ontogeny recapitulatory, one would expect ontogenetic reduction of trilacunar to unilacunar nodes. No seedling studied by Bailey displayed such reduction; on the contrary, first eophylls of a consider-able number examined were unilacunar succeeded by tri- or even multilacunar nodes. Unilacunar nodes are usually associated with exstipulate leaves, while tri-lacunar and multilacunar are associated with stipules (Carlquist, 1961).

Two is the common number of traces in the lower taxa of both dicots and monocots, but four or three by fusion of the middle pair are frequent. Large numbers seem uncommon but occur in some *Araceae* and *Cannaceae.* In many monocots there are two strong lateral traces supplying the sides of the sheathing leaf base.

According to Eames (1961), the vascular cylinder of primary roots of seed-lings is commonly diarch or tetrarch. Monarchy is rare in primary roots. Polyarchy

is frequent in monocotyledons. Tetrarchy has been considered more primitive than diarchy because of association with woody types, as for example in the *Fabaceae*. In Ranales, the *Ranunculaceae* have diarch while woody families have tetrarch primary roots. In *Asteraceae* both types occur, with neither obviously associated with primitive types. In dicots there are few variations from tetrarchy and diarchy, but in monocots, polyarchy with 4, 6, 8, or 12 poles is not uncommon.

COTYLEDON NUMBER It has been suggested by Eames (1961) that dicotyly is the rule among angiosperms and gymnosperms, and that such features as polycotyly, schizocotyly, anisocotyly, gamocotyly, monocotyly, and cryptocotyly are derived. Pseudomonocotylar embryos may result from the conferruminate (gamocotylar) condition as in *Eugenia, Nelumbo, Rhizophora,* etc., or from reduction of one of the cotyledons, as in species of *Abronia, Carum, Claytonia, Corydalis, Cyclamen, Dicentra, Eranthis, Erigenia, Mammillaria, Peperomia, Pinguicula, Ranunculus, Scaligera, Trapa,* etc. Cronquist (1968) notes in *Peperomia* a gradual differentiation of two cotyledons for different functions: *P. pellucida* has two equal cotyledons which are withdrawn to become the first functional leaves of the seedling; *P. peruviana* also has two, but only one is withdrawn from the seed, the other remains to function as an absorbing organ; *P. parvifolia* has two initially unequal cotyledons — the larger remains within the seed coat as an absorbing organ, the smaller becoming the first leaf of the seedling, a situation hardly to be distinguished from that in many monocots. In some *Gesneriacae,* the cotyledons are the only leaves the plant develops. Among monocots, some *Alismataceae, Araceae, Commelinaceae,* and *Dioscoreaceae* show rudiments of a second cotyledon. Anisocotyly is well exemplified by such embryos as *Petiveria.*

Tricotyly is a frequent aberration, occurring in such diverse plants as coffee, maple, mesquite, and walnut. Polycotyly has been reported for 2 to 4 percent of the "British flora" (Eames, 1961), and is frequent in parasitic dicots, e.g., *Loranthus, Nuytsia,* and *Persoonia.* In woody Ranalean taxa, the percentage of tricotylar embryos may reach as high as 87 percent, with 13 percent tetracotylar and none dicotylar (Eames, 1961). In some cases, e.g., conifers and crucifers, the two cotyledons may be so deeply lobed as to appear tetracotylar. In *Podocarpus coriaceus* (Duke, 1965a), the first pair of leaves is attached so close to the cotyledonary node as to give the seedling a tetracotylar appearance. Superficially the cotyledons and eophylls appear similar but the cotyledons have two veins prominent while the eophylls have only one.

Lobing of the cotyledons appears to be constant in some taxa such as *Bursera, Dacryodes, Lepidium,* and *Tilia* where the lobing is palmate and in *Amsinckia, Eschscholzia, Eucalyptus, Haematoxylum, Ipomoea, Pittosporum, Pterocarya,* and *Schizopetalon,* where the cotyledons are deeply bifid. Retuse cotyledons are more or less characteristic of *Bignoniaceae* and *Convolvulaceae.* Lobed cotyledons are not necessarily correlated with lobed leaves. Peculiar combinations such as trifoliolate cotyledons and entire eophyll 1 *(Bursera),* entire cotyledons, and trifoliolate eophyll 1 *(Ceiba),* bilobate cotyledons and paripinnate eophyll 1 *(Haema-*

toxylum), retuse cotyledons and imparipinnate eophyll 1 (*Jacaranda*) can be very diagnostic.

Plicate, crenate cotyledons seem to be characteristic of the arboreal segregates of the *Boraginaceae*. Glandular margins occur on the cotyledons of several seedlings whose adult leaves also have glandular margins (*Rosaceae*, *Rutaceae*, etc.).

Cotyledon

SHAPE AND SIZE Among entire cotyledons, there is a great variety of shapes and sizes which may be useful in determinations. Linear cotyledons are exceptional in some families, e.g., *Dodonaea* in *Sapindaceae*, and *Spondias* in *Anacardiaceae*, while they are the rule in others, especially in monocots and several dicots possessing "linear" embryos. Reniform cotyledons prevail in some families, especially those with "folded" and "spatulate" embryos (e.g., *Bignoniaceae*, *Combretaceae*, and *Malvaceae*). Many genera have species with narrow and species with broad cotyledons, e.g., *Coreopsis* and *Galium*.

Broad cotyledons are not necessarily followed by broad leaves. *Coccoloba*, *Fagus*, *Gomidesia*, *Hakea*, and *Myrcia* have species in which the cotyledons are broader than long while the eophylls are longer than broad. Other species have very narrow cotyledons followed by broad eophylls, e.g., *Acer*, *Cissampelos*, *Cochlospermum*, and *Menispermum*. Absolute size of the expanded cotyledons is probably less important than relative size.

Auriculate cotyledons occur (e.g., many *Fabaceae* and *Meliaceae*) while integrading cordate cotyledons seem less frequent (e.g., some *Ranunculaceae*). Peltate cotyledons occur but rarely (e.g., *Peperomia*), peltate eophylls being more frequent (e.g., *Hernandiaceae*, *Menispermaceae*, *Piperaceae*, and *Tropaeolaceae*).

COTYLEDON VENATION Bailey (1956) notes than many cotyledons are characterized by having a pseudo-palmate or palmate-parallel venation. Such cotyledons, scored *plinerved* in the polyclave, commonly have three or more conspicuous primary veins that extend outward from a locus at the base of the cotyledons, the laterals diverging and often reconverging parallel to the margins. Many such cotyledons show a transition from an even number (2) of vascular strands at the nodal level to an odd number (3 or 5) of primary veins in the lamina. There are numerous deviations from this common type, even among seedlings of the same genus or species. Cotyledons with different forms and venations may have similar basal (nodal) vasculatures and conversely cotyledons of similar form may have different nodal patterns.

Pinnate venation is less frequent in cotyledons than in foliage leaves, but there are more penninerved cotyledons among those attached at a single-trace node. Parallel venation is the common type in monocotyledons. In cryptocotylar forms, whose cotyledon tips are modified for suctorial purposes (*scutellum*), there is usually only one trace which divides to form a median and two strong lateral bundles, but only the median vein continues to the scutellum. In more primitive forms, in which there is little or no downbending of the distal part, all the vascular bundles, including those of the sides of the sheath, usually continue into the scutellum.

Carlquist (1961) notes that seedling anatomy is adduced as evidence of the origin of monocots from dicots but adds that vascular anatomy of cotyledons is perhaps of little significance because the duality of traces in each dicot cotyledon is as frequent as the well-known duality of traces in monocot cotyledons. The conservative nature of seedling anatomy promises useful evolutionary studies.

Cotyledons with a pair of midveins, as are frequent in gymnosperms like *Podocarpus coriaceus*, are only occasional in angiosperms (some *Austrobaileyaceae, Chloranthaceae, Monimiaceae,* and *Poaceae*). Examples of cotyledons and eophylls exhibiting similar venation patterns are rare.

In the polyclave the term *seed leaf* is used for the cotyledons after germination.

VERNATION Vernation (prefoliation) is the disposition of the leaves in the bud. The terminology in existence may be applied also to the relation of the cotyledons to each other in the seed. The types of vernation are:

Conduplicate induplicate: The lamina is folded lengthwise along the veins so that the halves of the *upper* surface lie together. This type is prevalent in leaves, but rare in cotyledons. The cotyledons of *Avicennia* are conduplicately folded, one so that its lower surfaces are opposed (reduplicate), the other induplicately embracing it (Duke, 1965a). *Monniera, Raphanus,* and other genera with orthoplocal embryos are similar to *Avicennia.*

Conduplicate reduplicate: The lamina is folded lengthwise along the veins so that the halves of the lower surface lie together as in some palm eophylls.

Plicate (pleated): The lamina is folded along the veins, like a closed fan, as in cotyledons of *Cordia* (Duke, 1965a), and in leaves of *Acer.*

Convolute: The lamina is rolled lengthwise forming a coil as in the leaves of certain *Rosaceae* and the cotyledons of many *Combretaceae* as in *Terminalia* (Duke, 1965a). According to Lubbock (1891) leaves of *Drimys, Kadsura,* and *Schisandra* are convolute. Among Asian mangroves, *Rhizophora* and *Bruguiera* have convolute vernation of the leaves, while *Carallia, Ceriops, Gynotroches,* and *Pellacalyx* have involute vernation.

Involute: Both margins of the lamina are inrolled lengthwise on the *upper* surface, as in certain *Violaceae* and *Rhizophoraceae.*

Revolute: Both margins of the lamina are inrolled lengthwise on the *lower* surface, as in many *Ericaceae.*

Reclinate (inflexed): The upper part of the blade is bent on the lower, as in leaves of *Liriodendron.* One of the cotyledons of *Petiveria* in addition to being involute, is doubled back on itself. The second broader cotyledon is convolute or involute about the first. It seems that the scutellum could in many cases represent the end of a reclinate cotyledon.

Circinate: The upper part of the blade is rolled back on the lower, so that the tip is in the center of the coil, as in *Cycadaceae* and *Droseraceae.* Certain legume eophylls, e.g., *Parkia* (Duke, 1965a), approach this type of vernation, while the cotyledons of *Cariniana* (Fig. 66) have a complex circinate vernation.

Strict: The blade is straight in the bud and expands by growth alone as in many cotyledons and adult leaves.

Vernation of the cotyledons frequently differs from that of eophylls. Major mangrove genera of Panama may be distinguished by virtue of vernation and eophyll arrangement alone. The distinguishing characters are:

Cotyledons strict; leaves involute ..... *Pelliceria*
Cotyledons not strict; leaves not involute:
  Cotyledons conduplicate ..... *Avicennia*
  Cotyledons convolute or conferruminate:
    Cotyledons conferruminate; leaves convolute ..... *Rhizophora*
    Cotyledons convolute; leaves not convolute:
      Eophylls opposite ..... *Laguncularia*
      Eophylls alternate ..... *Conocarpus*

PETIOLES AND STIPULES Sessile and long-petiolate cotyledons may occur on seedlings of the same genus or family, but there is rarely much variability at the specific level. In *Bryonia dioica* the cotyledons are long-petiolate while in *B. laciniosa* they are subsessile. Lubbock (1892) speculates that cotyledons tend to be sessile when they are supported by a long hypocotyl, but long-petiolate when borne close to the ground, citing *Vitis hypoglauca* with short hypocotyls and long cotyledonary petioles and *V. cebennensis* with long hypocotyl and short petioles. Petioles are often connate at the base as in *Lupinus, Podophyllum,* and *Sanguisorba.* On eophylls, the geniculate or incrassate petiole often foreshadows a compound leaf.

Stipules offer good diagnostic characters. Even the cotyledons of certain seedlings, e.g., in *Caesalpiniaceae, Fabaceae, Mimosaceae,* and *Rubiaceae,* have obvious stipules. The cotyledons of *Prosopis juliflora,* in addition to being stipulate, exhibit the nyctinastic tendencies of the foliage leaves. Among some cryptocotylar legumes, e.g., *Erythrina* spp., (Duke, 1965a), the cataphylls tend to have paired stipules almost equal to those of the eophylls. Stipules of the second eophyll of *Acacia farnesiana* are spinescent (Duke, 1965a). In stipulate plants, the stipules are usually apparent no later than the second eophyll stage. Stipules are usually apparent on the seedlings but absent from mature branches of species with fugaceous stipules. Stipels are obvious on the first eophylls of some *Mimosaceae* and *Moringaceae,* and may be expected in other families whose foliage leaves are characterized by stipels.

INDUMENT Presence or absence of indument is not highly definitive, but certain types of indument can be very useful in defining seedlings. Indument provides a main clue for distinguishing three weed-tree species' seedlings in Panama. Eophylls of *Cecropia* have a white arachnoid indument on the lower surface, while those of *Didymopanax* have a diffuse, more or less colorless indument. *Ochroma* eophylls have a close felted grayish indument, rusty at the base of the petioles (Duke, 1965a).

Punctate cotyledons are characteristic of several families *(Elaeagnaceae, Malvaceae, Myrtaceae, Primulaceae, Rutaceae).* Beneath a tree of *Thespesia populnea* near Guanica, Puerto Rico, where seedlings similar to those of *Ipomoea hispida,* as figured by Lubbock (1892). Examination with a lens showed the characteristic pellucid punctation of *Thespesia's* cotyledons, showing that this was merely an aberrant type with bifid cotyledons such as occur normally in *Ipomoea* spp. This is apparently the first such aberration reported for the *Malvaceae. Montezuma,* another malvaceous genus in Puerto Rico, often coexistent with *Thespesia,* may be distinguished on basis of its stellate hairs.

MICROSCOPY When critical determinations are needed, microscopic examination of the seedling will yield further clues. It has been generally agreed that the stomata on various plant parts are of the same type, but Paliwal and Bhandari (1962) point out that "The stomata on the leaves of *Michelia* and *Magnolia* are syndetocheilic while those occurring on the outer integument of ovules . . . are of the haplocheilic type." Stomatal types in cotyledons and in adult leaves could also differ; the point deserves investigation. It would be worthwhile to see if distribution of stomata is the same in cotyledons, eophylls, and adult foliage. Hydathodes or glandular mucrons are frequent at the tips of the cotyledons as in *Rhus typhina.*

EOPHYLL SEQUENCE Tomlinson (1960) proposed the term "eophyll" for the first few leaves with green, expanded laminae developed by the seedlings, as opposed to the brown rudimentary scale leaves of fixed number which precede them in most cryptocotylar species. In palms, he noted that the shape and size of the first eophyll is constant and the distribution of its armature and indument is diagnostic. Each palm has its characteristic series of transitional leaves between the eophylls and adult leaves. Similarly characteristic eophyll sequences occur in *Anacardiaceae, Bignoniaceae, Caesalpiniaceae, Fabaceae, Meliaceae, Mimosaceae, Sapindaceae,* etc., probably in most seedlings whose adults have compound leaves. The eophyll sequence may be abrupt, as in many *Mimosaceae* with the first eophyll pinnate, the second bipinnate; or delayed, as in many woody *Fabaceae, Meliaceae, Sapindaceae,* etc., where several eophylls are simple and succeeding ones gradually add leaflets. Often the tumid petiole of an eophyll foreshadows a compound leaf. In some species, there is no sequence, e.g., in *Guaiacum,* where paripinnate eophylls immediately follow the cotyledons (Duke, 1965a).

There are few reverse sequences in which eophylls are compound and adult leaves simple *(Acacia, Ulex).* I suspect this would prove to be true of *Swartzia* sp. (Fig. 22). In *Bursera simaruba,* the cotyledons are trifoliolate, eophylls simple, and adult leaves compound. In others, the cotyledons are lobate and the eophylls and adult leaves (metaphylls) simple *(Tilia).* Having cotyledons and eophylls precisely similar, as reported in *Dowingia* by Lubbock (1892) seems to be quite exceptional. There are few phanerocotylar species with cotyledons broader than the first 12 eophylls (*Asclepiadaceae, Cactaceae, Casuarinaceae, Myrtaceae, Proteaceae,* e.g.). Several species are known where the eophylls are more conspicuously dentate or lacerate than the adult leaves (*Casearia* sp., *Cordia* spp., *Ficus, Gustavia* (Fig. 65), *Quercus,* certain members of *Quiinaceae,* and *Rapanea* sp.).

Although the eophyll sequence is usually constant, Lubbock (1892) notes a remarkable amount of variation in *Ulex europaeus*. In some seedlings, the leaves are all simple, in others the primary leaves are simple, subsequent ones trifoliolate; in still others all leaves are trifoliolate. They may be alternate or opposite indiscriminately. All ultimately become modified into simple spines or may be altogether aborted, while the branches form compound or branching spines. Although there are exceptions, the eophyll sequence seems to be characteristic of the species, as do most other characters used to distinguish seedlings. Blastogeny may be added to the other exciting and relatively unexplored fields of investigation, where both variations and constancy may be used in evaluating taxonomic and systematic concepts. Even variability, e.g., heterophylly, as in *Morus, Sassafras,* and, in Panama, *Roupala,* seems to be a constant attribute of some taxa.

Preliminary Systematic Survey[1]

The following descriptions are based on the limited information available, mostly from the author's researches except where otherwise noted. Regrettably, the family description is often based on a single species. To amplify these studies, seeds are requested from any tropical American woody species accompanied by a voucher specimen. Especially desired are representatives of families not included in this paper, then genera, then species. When possible, the seeds will be germinated, illustrated, preserved in the seedling herbarium, with duplicate seedlings returned to the collector who will be duly acknowledged. Herbarium specimens from Latin America are available in exchange for those seeds accompanied by voucher specimens.

PODOCARPACEAE: Germination phanerocotylar, the two cotyledons linear, binervate. Eophylls pseudocotyledonary, like the cotyledons, but uninervate.

GNETACEAE: Seeds broadly oblongoid, the outer coat pinkish-red, not striped, the inner coat olive-brown, longitudinally striped. Germination cryptocotylar, with alternate cataphylls (Fig. 1).

ARECACEAE (PALMAE): Germination cryptocotylar. Cataphylls alternate. Eophylls simple, bifoliolate, or paripinnate; usually possessing the armature and indument of the adult. Vernation induplicate or reduplicate. The species illustrated (Figs. 2, 3, 4) all have bifoliolate eophylls. *Astrocaryum* eophylls are already armed and glaucous like the metaphylls (Fig. 4). The specimen illustrated had been grazed by some herbivore.

ARACEAE: Germination cryptocotylar, the cataphylls alternate, linear-lanceolate, the first eophyll long-petiolate, hastate, spirally convolute (*Montrichardia,* Fig. 5).

SMILACACEAE: Germination cryptocotylar. Cataphylls alternate; eophylls alternate, with venation like the metaphylls (Fig. 6).

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[1] Presented at the Second Symposium on Amazonian Biota in Florencia, Colombia, January 23, 1969, and submitted for publication in Spanish in the proceedings of the symposium.

CASUARINACEAE: Germination phanerocotylar, the cotyledons narrowly obovate; eophylls verticillate, appressed.

PIPERACEAE: Germination phanerocotylar to subcryptocotylar, monocotylar, anisocotylar, dicotylar, or tricotylar; the cotyledons sometimes retuse. Eophylls usually with aroma, indument, and venation of the metaphylls.

MORACEAE: Germination cryptocotylar (usually in large-seeded species, Figs. 7 and 8) with alternate cataphylls to phanerocotylar (usually in small-seeded species like *Ficus,* Fig. 9) without cataphylls, often anisocotylar. Latex, stipules, and indument often characteristic. Eophylls in cryptocotylar species alternate, stipulate, often more conspicuously dentate than the metaphylls, as in *Brosimum bernadettae* (Fig. 8) [but entire and with caducous stipules in *B. utile* (Fig. 7)]. *Cecropia* and *Pourouma* suggest transitions to *Urticaceae.*

CANNABACEAE: Germination phanerocotylar; the cotyledons sessile, entire, uninerved, or triplinerved. Eophylls near the cotyledons, subsessile, penninerved, with an undulate, rugulose margin, sometimes basally dentate (Fig. 10).

URTICACEAE: Germination phanerocotylar, often anisocotylar. Cotyledons long-petiolate, often plinerved and reniform. Indument, venation, and arrangement of the eophylls often diagnostic.

OLACACEAE: Germination cryptocotylar, the stalked cotyledons secund. Hypocotyl glabrous, somewhat swollen. Cataphylls alternate, the upper subtended by spines, grading into alternate, penninerved, glabrous, entire, mucronate eophylls, subtended by spines *(Ximenia).*

POLYGONACEAE: Germination phanerocotylar, the two cotyledons reniform, subplinerved. Eophylls supracotyledonary, alternate, subconvolute, penninerved, ochreate *(Coccoloba).* My efforts to germinate *Triplaris* have failed. Peculiar that a weed-tree should possess such low vitality!

NYCTAGINACEAE: Germination phanerocotylar, at first anisocotylar, the cotyledons becoming subequal, subsessile, reniform, plane, entire, penninerved. Eophylls supracotyledonary, alternate, entire, short-petiolate, penninerved (*Neea;* Fig. 11).

ANNONACEAE: Germination phanerocotylar, often tardily so, probably cryptocotylar in large-seeded species. Cotyledons lanceolate, subpenninerved. Eophylls alternate, conduplicate. Aroma, indument, and venation often diagnostic.

MYRISTICACEAE: Germination cryptocotylar, the secund cotyledons borne in the corrugated seed well above the ground. Eophylls supracotyledonary, alternate, conduplicate, exstipulate, penninerved, entire (*Virola,* Fig. 12). Latex, indument, and aroma often diagnostic.

MONIMIACEAE: Germination phanerocotylar, the hypocotyl basally swollen, the cotyledons subsessile, broadly ovate, subplinerved and bluntly apiculate in *Mollinedia* (Fig. 13), uninerved and emarginate in *Siparuna* (Fig. 14).

LAURACEAE: Germination cryptocotylar, the epicotyl usually emerging from the cotyledons, i.e., cotyledons not secund. Cataphylls alternate. Eophylls alternate, entire, exstipulate, penninerved. Aroma and indument often diagnostic.

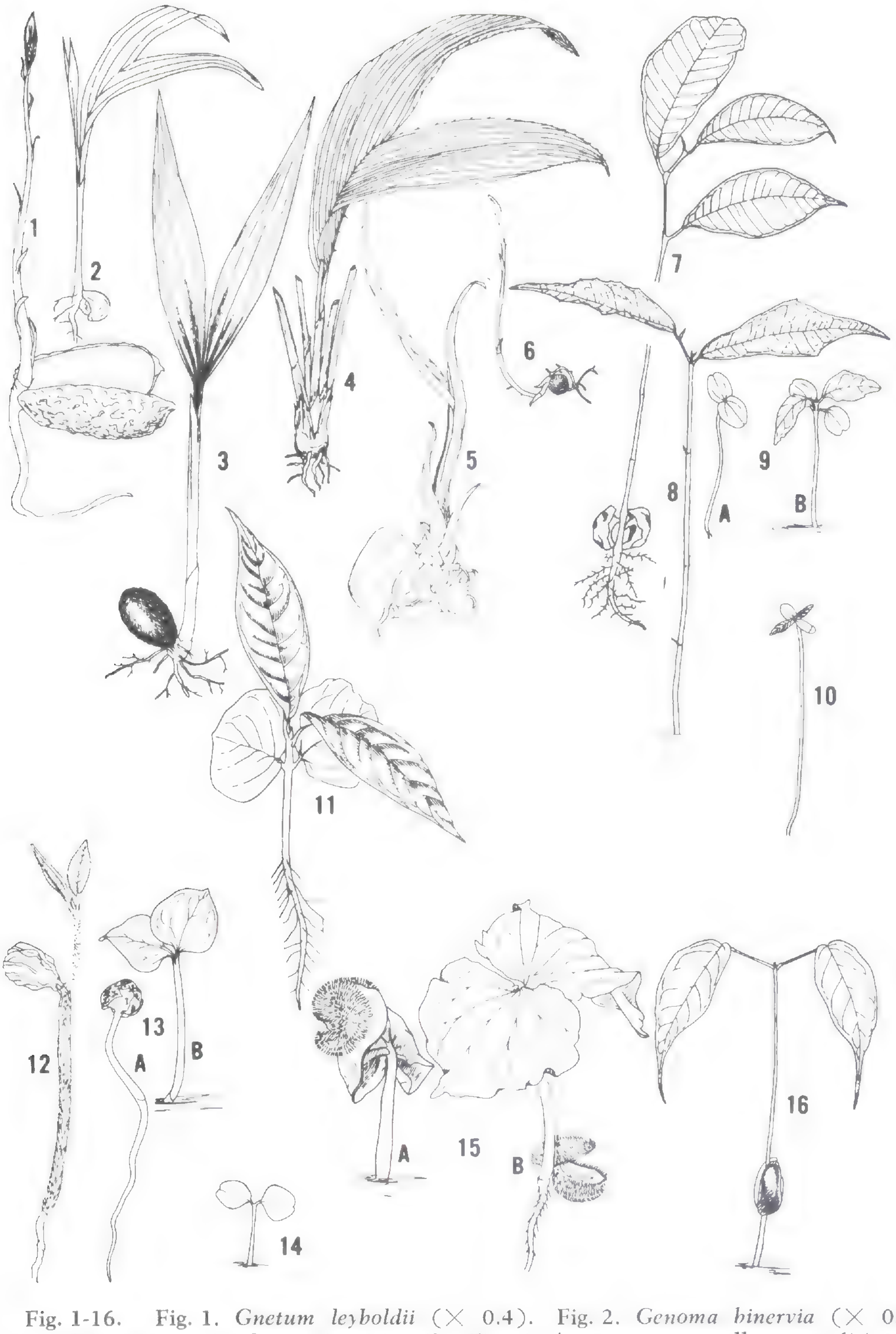

Fig. 1-16. Fig. 1. *Gnetum leyboldii* (× 0.4). Fig. 2. *Genoma binervia* (× 0.8). Fig. 3. *Welfia georgii* (*Duke 15030;* × 0.6). Fig. 4. *Astrocaryum standleyanum* (× 0.2). Fig. 5. *Montrichardia arborescens* (× 0.4). Fig. 6. *Smilax* sp. (*Duke 15077;* × 0.4). Fig. 7. *Brosium utile* (× 0.2). Fig. 8. *Brosium bernadetteae* (× 0.4). Fig. 9. *Ficus insipida* (*Duke 15195;* × 0.8). Fig. 10. *Cannabis sativa* (× 0.4). Fig. 11. *Neea* sp. (*Duke 15332;* × 0.4). Fig. 12. *Virola* sp. (× 0.4). Fig. 13. *Mollinedia* (*Duke 15234;* × 0.4). Fig. 14. *Siparuna* (*Duke 15128;* × 0.8). Fig. 15. *Capparis pittieri* (× 0.4). Fig. 16. *Connarus panamensis* (× 0.4).

HERNANDIACEAE: Germination cryptocotylar, the stalked cotyledons secund. Cataphylls alternate, grading into alternate, peltate, subplinerved, entire eophylls (*Hernandia*).

PAPAVERACEAE: Germination phanerocotylar, the cotyledons subsessile, elliptic, entire, plinerved. Eophylls cotyledonary, quercoid, with orange latex (*Bocconia*).

CAPPARACEAE: Germination phanerocotylar, the cotyledons plane or slightly planoconvex, subconvolute. Eophylls alternate, entire, penninerved, conduplicate. *Capparis pittieri* (Fig. 15) has the largest cotyledons of any *Capparaceae* studied, characteristically raising the gray pubescent testa with them. Several nerves arise at the base of the cotyledon and the hypocotyl is somewhat swollen.

MORINGACEAE: Germination cryptocotylar, the short-stalked cotyledons remaining in the trialate seed. First eophylls supracotyledonary, opposite, decompound, stipellate. As is often true in cryptocotylar species, the plumule is foliate in the ungerminated seed.

CHRYSOBALANACEAE: Germination cryptocotylar, the cotyledons secund. Cataphylls alternate, sometimes stipulate, grading into alternate, stipulate, entire, lanceolate to ovate, penninerved eophylls.

CONNARACEAE: Germination cryptocotylar, cataphylls *absent*. First eophylls supracotyledonary, opposite, often incrassipetiolate, ovate, subcordate, entire. *Connarus panamensis* (Fig. 16), like *Rourea,* resembles the seedlings of many *Fabaceae,* e.g., *Ormosia* (Fig. 23), and is often dormant at the stage depicted. The absence of stipules on the eophylls separates the *Connaraceae* from most *Fabaceae*.

MIMOSACEAE: Germination phanerocotylar to cryptocotylar, with or without cataphylls; eophylls simple to decompound, the sequence gradual to abrupt.

The species of *Inga* investigated, like *I. spectabilis* (Fig. 17), have nonphotosynthetic cotyledons, rarely secund, usually auriculate, which are cryptocotylar but escape from the testa shortly after germination. These seeds frequently germinate while still in the pod. Cataphylls are sometimes present, and stipulate. All first eophylls studied are bifoliolate.

Pithecellobium longifolium (Fig. 18) has seedlings comparable to *Inga,* subcryptocotylar with nonphotosynthetic cotyledons and bifoliolate eophylls. All species of *Pithecellobium* studied generate the odor of a mercaptan in germinating.

Cotyledons of *Pentaclethra* (Fig. 19) are somewhat similar, but are green and probably photosynthetic, usually gaping apart at the surface of the soil in the swamps they frequent, thus not exactly hypogeal nor epigeal, nor cryptocotylar nor phanerocotylar. The first eophylls are decompound.

CAESALPINIACEAE: Germination phanerocotylar to cryptocotylar, with or without cataphylls, cryptocotylar cataphylliferous germination usually associated with the larger seeds. Probably the most affirmative demonstration of the importance of seedlings to systematics is Léonard's (1957) excellent work on African *Caesalpiniaceae,* in which he proposes the following hypotheses:

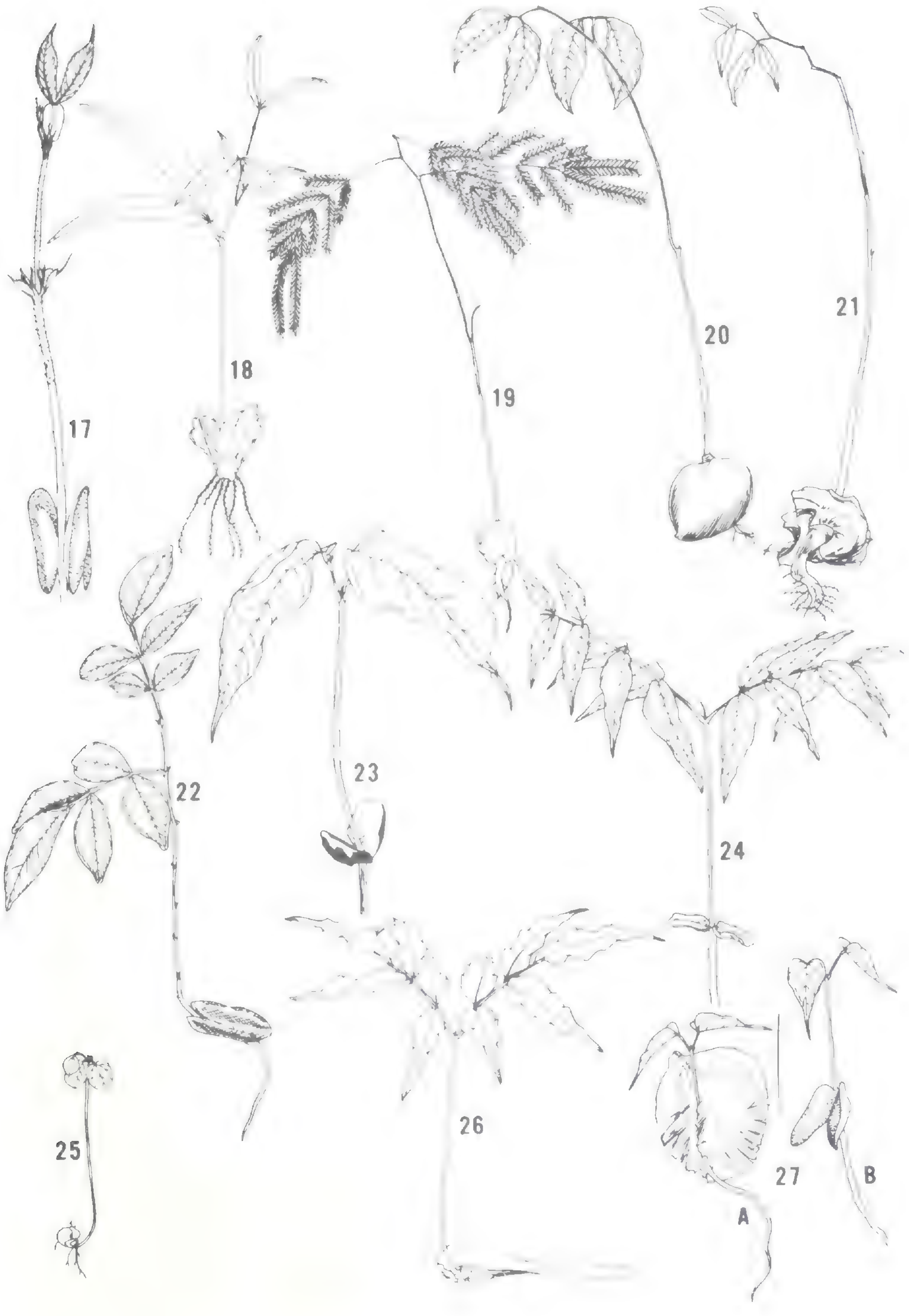

Fig. 17-27. Fig. 17. *Inga spectabilis* (× 0.4). Fig. 18. *Pithecellobium longifolium* (*Duke 8212;* × 0.8). Fig. 19. *Pentaclethra macroloba* (× 0.1). Fig. 20. *Prioria copaifera* (× 0.1). Fig. 21. *Mora oleifera* (× 0.04). Fig. 22. *Swartzia simplex* (× 0.4). Fig. 23. *Ormosia* sp. (× 0.4). Fig. 24. *Oleiocarpon panamensis* (× 0.2). Fig. 25. *Maughania* sp. (*Duke 15448;* × 0.4). Fig. 26. *Myroxylon balsamum* (× 0.4). Fig. 27. *Pterocarpus hayesii* (× 0.4).

(a) The establishment of synonymy between genera according to morphological data should be provable by the similarity of their seedlings.

(b) Morphologically related genera, which have the same seedlings, may not be generically distinct.

(c) The partition of a heterogeneous genus into several genera according to their morphological characters, should be provable by the existence of a particular seedling type for each of them.

(d) The existence of several seedling types within one genus may be an indication of a generic heterogeneity that must be checked by other morphological data.

Prioria copaifera (Fig. 20), a swamp forest species, is cryptocotylar with alternate cataphylls succeeded by bifoliolate eophylls which gradually give way to paripinnate metaphylls.

Mora oleifera (Fig. 21), a brackish swamp forest species, with the largest dicot seeds known, is also cryptocotylar with alternate cataphylls succeeded by bifoliolate eophylls succeeded by paripinnate metaphylls.

FABACEAE: Germination phanerocotylar to cryptocotylar, with or without cataphylls (in the same genus occasionally). Cataphylls often stipulate. Simple incrassipetiolate eophylls often foreshadow compound metaphylls. Latex, indument, stipules, stipellae, leaf margin, venation, and arrangement often diagnostic.

Cryptocotylar *Swartzia* (Fig. 22) exhibits the rare reversed eophyll sequence, the imparipinnate eophylls gradually giving way to unifoliolate metaphylls.

Ormosia (Fig. 23) is barely phanerocotylar, the nonphotosynthetic cotyledons often embraced by the nigrescent testa.

Oleiocarpon panamensis (Fig. 24) exhibits an abrupt sequence, the phanerocotylar cotyledons being followed by eophylls similar in structure to the metaphylls.

Maughania, an introduction becoming a regular constituent of the savanna flora, is cryptocotylar, apparently without cataphylls, the eophylls unifoliolate (Fig. 25).

Myroxlon (Fig. 26) is cryptocotylar, without cataphylls, with the first imparipinnate eophylls opposite. This combination of characters shows up in several families with alternate leaves and cryptocotylar seedlings: (1) Species which have cataphylls have the first eophylls alternate while (2) species without cataphylls have the first two eophylls opposite, with subsequent eophylls alternate.

The seedling of *Pterocarpus hayesi* (Fig. 27) resembles that of *P. indica* more than that of *P. officinalis*. It differs from both in having the first eophylls opposite. It is transitional from cryptocotyly to phanerocotyly. Some cotyledons, probably photosynthetic, emerge from the seed but remain secund, others apparently never escape from the seed.

ERYTHROXYLACEAE: Germination phanerocotylar, the cotyledons oblong, uninerved. Eophylls alternate, supracotyledonary, entire, penninerved, convolute, usually stipulate.

ZYGOPHYLLACEAE: Germination phanerocotylar, the cotyledons subsessile, subtriplinerved, entire, elliptic, glabrous. First eophylls supracotyledonary, opposite, paripinnate *(Guaiacum)*.

RUTACEAE: Germination cryptocotylar to phanerocotylar, often anisocotylar. Cotyledons and eophylls often aromatic and punctate, a marginal row of glands frequent. Eophyll sequence gradual in compound-leaved species. Polyembryony frequent.

Citrus limonum (Fig. 28) is cryptocotylar, anisocotylar, the cotyledons secund; the eophylls are alternate, punctate, dentate, penninerved, with alate, armed petioles.

Murraya (Fig. 29) is cryptocotylar with alternate cataphylls and dentate, aromatic eophylls.

SIMARUBACEAE: I have not yet observed germination in *Quassia* (Fig. 30) but suspect it is cryptocotylar. The eophylls suggest certain *Mimosaceae, Caesalpiniaceae,* and *Sapindaceae.*

BURSERACEAE: Cotyledons contortuplicate and subcryptocotylar *(Dacryodes)* to simple and planoconvex *(Tetragastris, Protium)* or trifoliolate *(Bursera)* and phanerocotylar. First eophylls simple and opposite *(Protium, Tetragastris)* or alternate (*Bursera,* sporadically bifid) to trifoliolate and opposite *(Dacryodes)*. Aroma often diagnostic. *Tetragastris panamensis* (Fig. 31) is similar to *T. balsamifera* with auriculate apiculate cotyledons, the eophylls opposite, supracotyledonary, penninerved, entire, or basally auriculate.

MELIACEAE: Germination cryptocotylar with alternate cataphylls and eophylls *(Swietenia)* or with no cataphylls and opposite, entire to dentate eophylls *(Guarea, Trichilia)* to phanerocotylar *(Melia, Cedrela)*.

Carapa (Fig. 32) conforms to the *Guarea-Trichilia* type.

Cedrela (Fig. 33) has subsessile, entire, plane, narrowly ovoid cotyledons, with alternate, supracotyledonary, trifoliolate, often dentate, eophylls.

Melia (Fig. 34) has petiolate, obovoid, triplinerved, entire cotyledons with the aceroid first eophyll apparently borne at the cotyledonary node.

Trichilia cipo (Fig. 35) differs from other species in that the cotyledons separate but are not strictly opposite or secund.

MALPIGHIACEAE: Germination cryptocotylar (especially in alate seeds) without cataphylls to phanerocotylar, often tardy (1 year in *Byrsonima*). Eophylls alternate to opposite, exstipulate, entire, penninerved, the indument often diagnostic.

Although germination in *Bunchosia* (Fig. 36) is phanerocotylar, the greenish-white, planoconvex, subsessile cotyledons are probably not photosynthetic. Although I found hundreds of these seedlings beneath a parent tree on San Jose Island and all had aerial cotyledons ("epigeal") I believe that, if the seeds were planted beneath the surface of the soil, the cotyledons would not emerge ("hypogeal"). The eophylls are supracotyledonary, opposite, decussate, entire, penninerved, pubescent.

POLYGALACEAE: Germination cryptocotylar, the subsessile cotyledons secund. Cataphylls alternate, grading into the alternate, entire, narrowly ovate eophylls *(Securidaca)*.

EUPHORBIACEAE: Germination mostly phanerocotylar with long-petiolate cotyledons, subcryptocotylar in *Hura* and cryptocotylar in *Hevea,* both, however with long-petiolate, secund cotyledons. Eophyll type, arrangement, indument, venation, glands, and latex often diagnostic.

Hippomane already has poisonous latex at the stage illustrated in Fig. 37. The cotyledons, often cyanotic or bronze-colored, are entire, triplinerved, the petioles with a copious white latex. The first eophylls are supracotyledonary, opposite, dentate, penninerved, subsequent eophylls alternate and stipulate.

ANACARDIACEAE: Germination cryptocotylar *(Comocladia)* to phanerocotylar with secund [*Anacardium excelsum* (Fig. 38) and *A. occidentale*] or opposed cotyledons. Eophylls alternate *(Comocladia)*, opposite *(Spondias)* or pseudoverticillate *(Anacardium, Mangifera)*. Alternate cataphylls usually present in cryptocotylar species. Eophyll sequence gradual in compound-leaved species.

STAPHYLEACEAE: Germination phanerocotylar, the cotyledons subsessile, ovate, entire to retuse, subplinerved. First eophylls supracotyledonary, opposite, trifoliolate, stipulate, and stipellate, the leaflets denticulate. Eophyll sequence gradual *(Turpinia)*.

SAPINDACEAE: Germination cryptocotylar with alternate cataphylls and eophylls *(Allophylus, Meliococcus, Sapindus)* or without cataphylls and with the first eophylls opposite *(Cupania, Maytayba, Paullinia, Serjania, Thouinia)*; rarely phanerocotylar *(Dodonaea)*.

Talisia nervosa (Fig. 39) suggests *Meliococcus,* with cryptocotylar germination and alternate cataphylls and bifoliolate alternate eophylls.

SABIACEAE: Germination phanerocotylar, the cotyledons foliar, plane, entire to undulate, subsessile, penninerved. Hypocotyl swollen, glabrous. Eophylls supracotyledonary, alternate, dentate, penninerved (*Meliosma,* Fig. 40).

RHAMNACEAE: Germination phanerocotylar, the cotyledons equal, triplinerved, long-petiolate. First eophylls supracotyledonary, opposite, penninerved *(Colubrina)* or plinerved *(Zizyphus)*, subsequent eophylls alternate.

TILIACEAE: Germination phanerocotylar, often associated with the rotting fruit, the cotyledons petiolate, broadly obovate, basally subtruncate, triplinerved, entire (*Apeiba aspera,* Fig. 41).

MALVACEAE: Germination phanerocotylar, the cotyledons often convolute, reniform triplinerved to multiplinerved, long-petiolate, often punctate. First eophylls supracotyledonary, alternate, stipulate. Indument and venation often diagnostic.

Hibiscus coclensis (Fig. 42) illustrates the similarity between seedlings of *Tiliaceae* and *Malvaceae.*

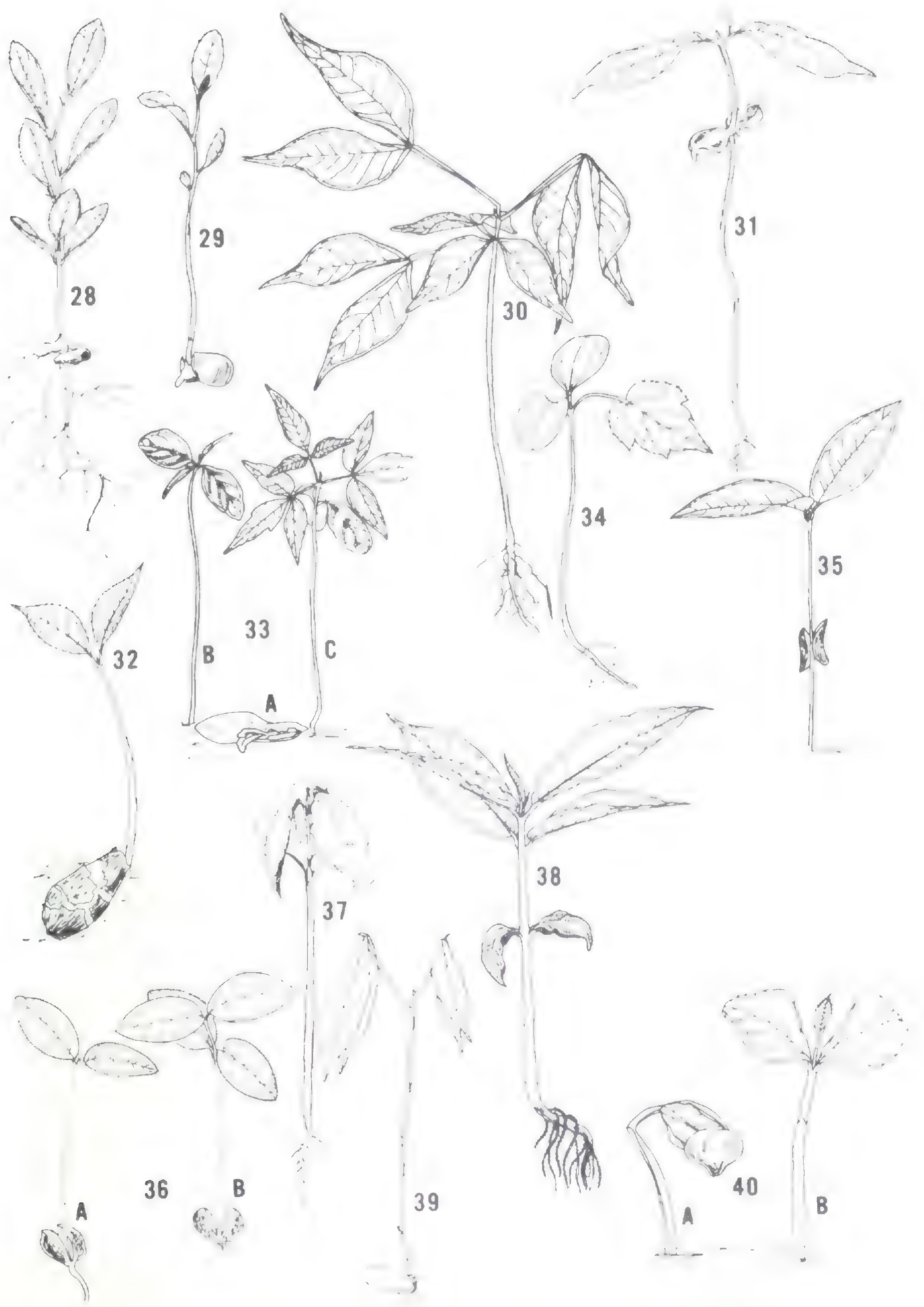

Fig. 28-40. Fig. 28. *Citrus limonum* (× 0.4). Fig. 29. *Murraya exotica* (× 0.6). Fig. 30. *Quassia amara* (× 0.4). Fig. 31. *Tetragastris panamensis* (× 0.4). Fig. 32. *Carapa* sp. (*Duke 14988;* × 0.4). Fig. 33. *Cedrela* sp. (× 0.4). Fig. 34. *Melia azederach* (× 0.8). Fig. 35. *Trichilia cipo* (× 0.4). Fig. 36. *Bunchosia cornifolia* (*Duke 15034;* × 0.4). Fig. 37. *Hippomane mancinella* (*Duke 11732;* × 0.4). Fig. 38. *Anacardium excelsum* (*Duke 8383;* × 0.3). Fig. 39. *Talisia nervosa* (×0.4). Fig. 40. *Meliosma panamensis* (× 0.4).

BOMBACACEAE: Germination cryptocotylar to phanerocotylar, the cotyledons ovate to reniform, subsessile to long-petiolate, subplinerved, the eophylls supracotyledonary, alternate, stipulate, the transition to compound leaves gradual. Hypocotyl often swollen, especially in those species destined to be "bottle trees."

Hampea (Fig. 43) illustrates the convolution of the emerging cotyledons.

Pachira is cryptocotylar with both the cataphylls and eophylls alternate (Fig. 44).

All *Quararibea* examined are cryptocotylar with alternate cataphylls but with the first pair of eophylls opposite or verticillate (Fig. 45). Dried seedlings have the odor characteristic of the adults.

Matisia cordata (Fig. 46) has rugulose, withered, probably nonphotosynthetic, phanerocotylar cotyledons, with the first eophylls opposite and stipulate.

STERCULIACEAE: Germination cryptocotylar to phanerocotylar, often in the same genus (*Sterculia, Theobroma*). Cotyledons convolute in phanerocotylar, secund in cryptocotylar, species of *Sterculia,* as e.g., *S. costaricense* (Fig. 47) and *S. apetala.*

DILLENIACEAE: Germination phanerocotylar, the cotyledons conduplicate, penninerved (*Doliocarpus,* Fig. 48).

OCHNACEAE: Germination phanerocotylar (often tricotylar), the cotyledons sessile, enervate, planoconvex, acuminate, often cyanotic, probably not photosynthetic. Eophylls supracotyledonary, alternate but appearing subverticillate, narrowly ovate, exstipulate, penninerved, more conspicuously dentate than the metaphylls (*Ouratea,* Fig. 49).

MARCGRAVIACEAE: Germination phanerocotylar, with little or no hypocotyl, the cotyledons subsessile, uninerved (Fig. 50). Although many seeds germinated, none showed development of the epicotyl. Developmental studies of the family should prove interesting.

PELLICERIACEAE: Germination subcryptocotylar, the exocarp falling away and exposing the reddish, sessile, planoconvex, nonphotosynthetic cotyledons. Eophylls supracotyledonary, alternate, involute, exstipulate, weakly nerved (*Pelliceria,* Fig. 51).

CLUSIACEAE: Germination cryptocotylar, the cotyledons secund, cataphylls supracotyledonary, opposite (in all genera studied except *Clusia* with phanerocotylar, submultiplinerved, equal cotyledons). Latex present in the youngest seedling studied.

Rheedia (Fig. 52) is characteristic of the cryptocotylar species, with opposite, deltoid cataphylls, followed by opposite, entire penninerved eophylls. The illustrated specimen took a year to germinate.

BIXACEAE: Germination phanerocotylar, the entire, ovate cotyledons weakly triplinerved, punctate-lineate. Eophylls supracotyledonary, alternate, ovate, subcordate, subplinerved, punctate-lineate (*Bixa,* Fig. 53).

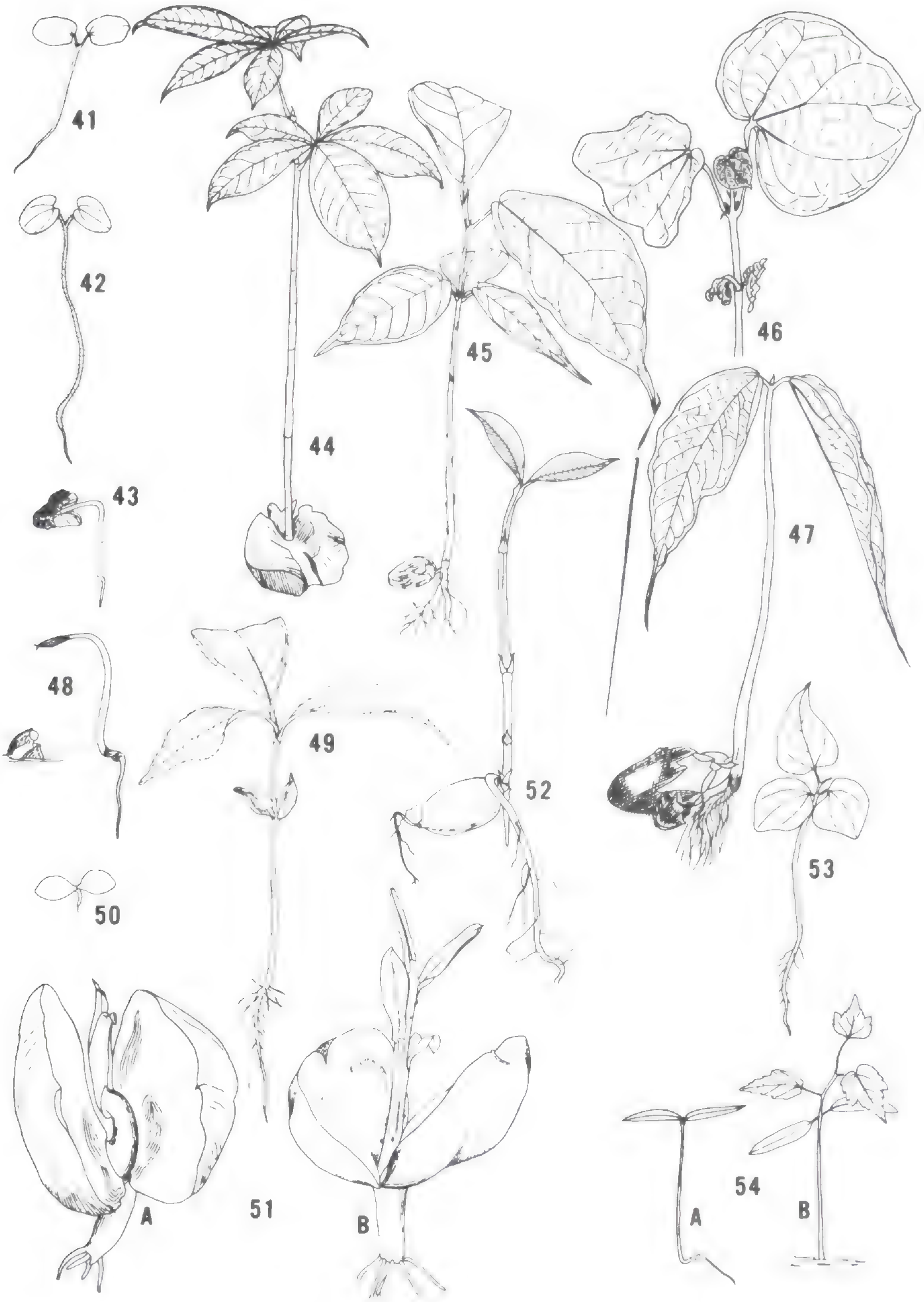

Fig. 41-54. Fig. 41. *Apeiba aspera* (× 0.8). Fig. 42. *Hibiscus cocleanus* (*Duke 13934*; × 0.8). Fig. 43. *Hampea* sp. (× 0.4). Fig. 44. *Pachira aquatica* (× 0.1). Fig. 45. *Quararibea asterolepis* (*Bristan 1335*; × 0.4). Fig. 46. *Matisia cordata* (× 0.2). Fig. 47. *Sterculia costaricana* (× 0.3). Fig. 48. *Doliocarpus* sp. (× 0.4). Fig. 49. *Ouratea lucens* (*Duke* 8298; × 0.4). Fig. 50. *Marcgraviaceae* (× 3.2). Fig. 51. *Pelliceria rhizophorae* (× 0.4). Fig. 52. *Rheedia* sp. (*Duke 11980;* × 0.4). Fig. 53. *Bixa orellana* (× 0.6). Fig. 54. *Cochlospermum vitifolium* (× 0.4).

COCHLOSPERMACEAE: Germination (after 1 year) phanerocotoylar, the cotyledons short-petiolate, linear-lanceolate, entire, uninerved. Eophylls supracotyledonary, alternate, aceroid. Latex orange (*Cochlospermum,* Fig. 54).

VIOLACEAE: Germination phanerocotylar, the cotyledons subsessile, entire, triplinerved, the eophylls supracotyledonary, alternate, penninerved, coarsely dentate [more so than metaphylls, stipulate (Duke No. 15005)]; or germination cryptocotylar, the cotyledons sessile, not secund, with subopposite cataphylls grading into subopposite eophylls (*Gloeospermum,* Fig. 55).

FLACOURTIACEAE: Germination phanerocotylar, the eophylls supracotyledonary, alternate, stipulate, penninerved, often pellucid-punctate or lineate, usually more conspicuously dentate than the metaphylls.

Mayna (Fig. 56) is a typical flacourtiaceous seedling.

PASSIFLORACEAE: Germination phanerocotylar, the cotyledons long-petiolate, elliptic, entire, plinerved, the eophylls supracotyledonary (Fig. 57), alternate, variable in shape and venation; less commonly cryptocotylar (Fig. 58).

CACTACEAE: Germination phanerocotylar, anisocotylar, the cotyledons subsessile, plane, broadly ellipsoid, entire, penninerved, ultimately becoming almost equal, with axillary spines; eophylls supracotyledonary, subopposite, tardily spinescent, rather like the cotyledons (*Pereskia,* Fig. 59).

The anisocotylar, planoconvex, linear cotyledons of *Wittia* (Fig. 60) are the only leaves on this epiphyte.

LECYTHIDACEAE: Apparently there are two germination types in Panama's *Couratari* (Fig. 61 and Fig. 62). Correa and Dressler No. 793 is phanerocotylar, the hypocotyl slightly tetragonal, the cotyledons ovate, rugulose but plane, penninerved. In *C. panamensis,* however, the cotyledons remain in the winged seed, followed by supracotyledonary eophylls, suggestive of the cotyledons in the phanerocotylar species. Cataphylls are absent.

The seedlings of *Eschweilera* (Fig. 63) and *Lecythis* (Fig. 64) conform to the *Gustavia* type (Fig. 65), cryptocotylar with alternate cataphylls and eophylls.

Gustavia superba (Fig. 65) is cryptocotylar, the epicotyl arising between the corrugated, planoconvex cotyledons, with alternate cataphylls, grading into alternate, exstipulate, lanceolate to oblanceolate eophylls, proportionately more dentate than the metaphylls.

Cariniana pyriformis (Fig. 66) has very distinctive phanerocotylar germination, the aceroid lobate cotyledons subcircinately embraced in the testa which is raised with the cotyledons. The drip-tips of the cotyledons are very conspicuous as they unfold. The eophylls are supracotyledonary, alternate, penninerved, and more conspicuously dentate than the metaphylls.

RHIZOPHORACEAE: Germination cryptocotylar, without cataphylls, the eophylls supracotyledonary, opposite, exstipulate, penninerved, entire, glabrous *(Rhizophora).*

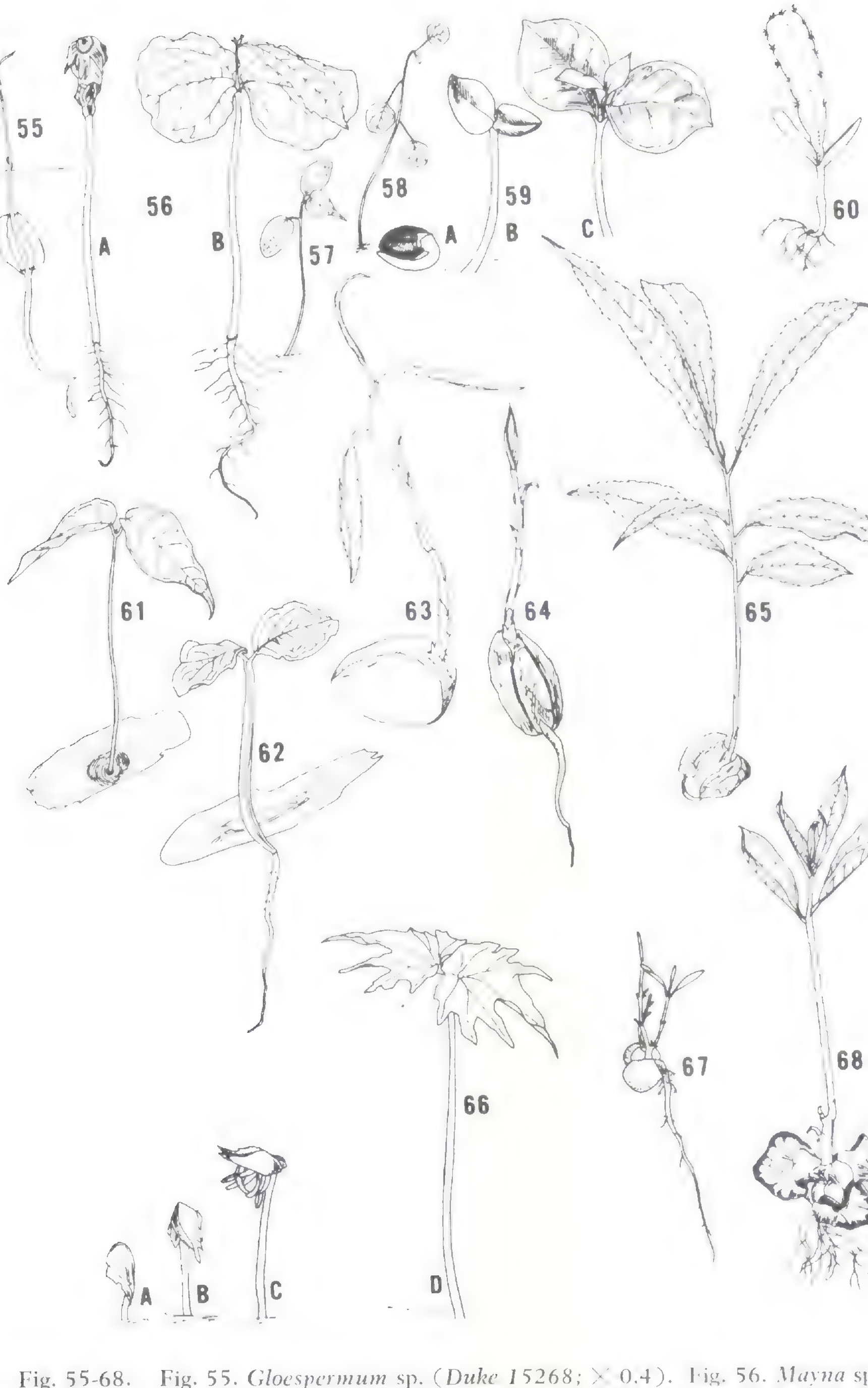

Fig. 55-68. Fig. 55. *Gloespermum* sp. (*Duke 15268*; × 0.4). Fig. 56. *Mayna* sp. (*Duke 14963*; × 0.4). Fig. 57. *Passiflora* sp. (*Duke 13270*; × 0.4). Fig. 58. *Passiflora* sp. (*Duke 15287*; × 0.4). Fig. 59. *Pereskia bleo* (A × 1.2; B & C × 0.4). Fig. 60. *Wittia* sp. (× 0.4). Fig. 61. *Couratari panamensis* (× 0.4). Fig. 62. *Couratari* sp. (*Correa & Dressler 793*; × 0.4). Fig. 63. *Eschweilera* (*Bristan 22*; × 0.4). Fig. 64. *Lecythis* sp. (*Blume s.n.* "monkey pot"; × 0.4). Fig. 65. *Gustavia superba* (× 0.1). Fig. 66. *Cariniana pyriformis* (× 0.4). Fig. 67. *Syzygium* sp. (*Duke 15302*; × 0.8). Fig. 68. *Eugenia malaccense* (× 0.4).

COMBRETACEAE: Germination phanerocotylar, the cotyledons reniform, convolute, the eophylls supracotyledonary, alternate or opposite, exstipulate.

MYRTACEAE: Seedlings, like the embryos, diagnostic for certain generic groups, cryptocotylar and often polyembryonic in those characterized by conferruminate planoconvex cotyledons (*Eugenia,* Fig. 68; *Syzygium,* Fig. 67) (cataphylls present or absent); phanerocotylar with broadly ovate subsessile cotyledons (*Gomidesia, Myrcia*), or with lanceolate, uninerved cotyledons (*Psidium*). Punctations, indument, and aroma are often diagnostic.

MELASTOMACEAE: Commonly the germination is phanerocotylar, the eophylls decussate with the cotyledons.

Mouriri parvifolia (Fig. 69), however, is cryptocotylar, the cotyledons secund in the testa, which is raised above the soil. Supracotyledonary, opposite cataphylls and eophylls are mostly borne in the same plane.

ARALIACEAE: Germination phanerocotylar, the cotyledons broadly ovate, plinerved to penninerved, the eophylls simple, often telescoped at the cotyledonary node; the eophyll sequence gradual.

MYRSINACEAE: Germination phanerocotylar, sometimes operculate, the cotyledons equal or anisocotylar, the margins entire or undulate, often punctate or lineate and cyanotic; eophylls usually supracotyledonary, alternate, conduplicate exstipulate (*Ardisia* spp., Figs. 70 and 71).

SAPOTACEAE: Germination cryptocotylar, without cataphylls but with secund cotyledons, to phanerocotylar, the cotyledons dark green and coriaceous. Eophylls usually supracotyledonary and alternate. Latex usually obvious at an early stage.

OLEACEAE: Germination phanerocotylar, the cotyledons subsessile; eophylls supracotyledonary, opposite.

APOCYNACEAE: Germination usually phanerocotylar, the cotyledons ovate, cordate to auriculate, triplinerved. Eophylls supracotyledonary, alternate, lanceolate to oblanceolate, entire, penninerved. Latex copious (*Plumeria*).

Lacmellea edulis (Fig. 72) is cryptocotylar, the stalked cotyledons secund; cataphylls opposite, eophylls lanceolate, opposite, weakly nerved. Latex copious, sticky, white.

Stemmadenia (Fig. 73) has phanerocotylar, ovate, entire to undulate, glabrous, penninerved, subsessile cotyledons with copious latex, the eophylls supracotyledonary, entire, penninerved, decussate with the cotyledons.

ASCLEPIADACEAE: Germination phanerocotylar, the elliptic cotyledons long-petiolate, penninerved, with white latex. First eophylls supracotyledonary, opposite (*Calotropis*).

CORDIACEAE: Germination phanerocotylar, the cotyledons deltoid, subsessile to long-petiolate, plicate, undulate to crenulate. Eophylls supracotyledonary, alternate, penninerved, usually more prominently dentate than the metaphylls. Cystoliths and indument often diagnostic.

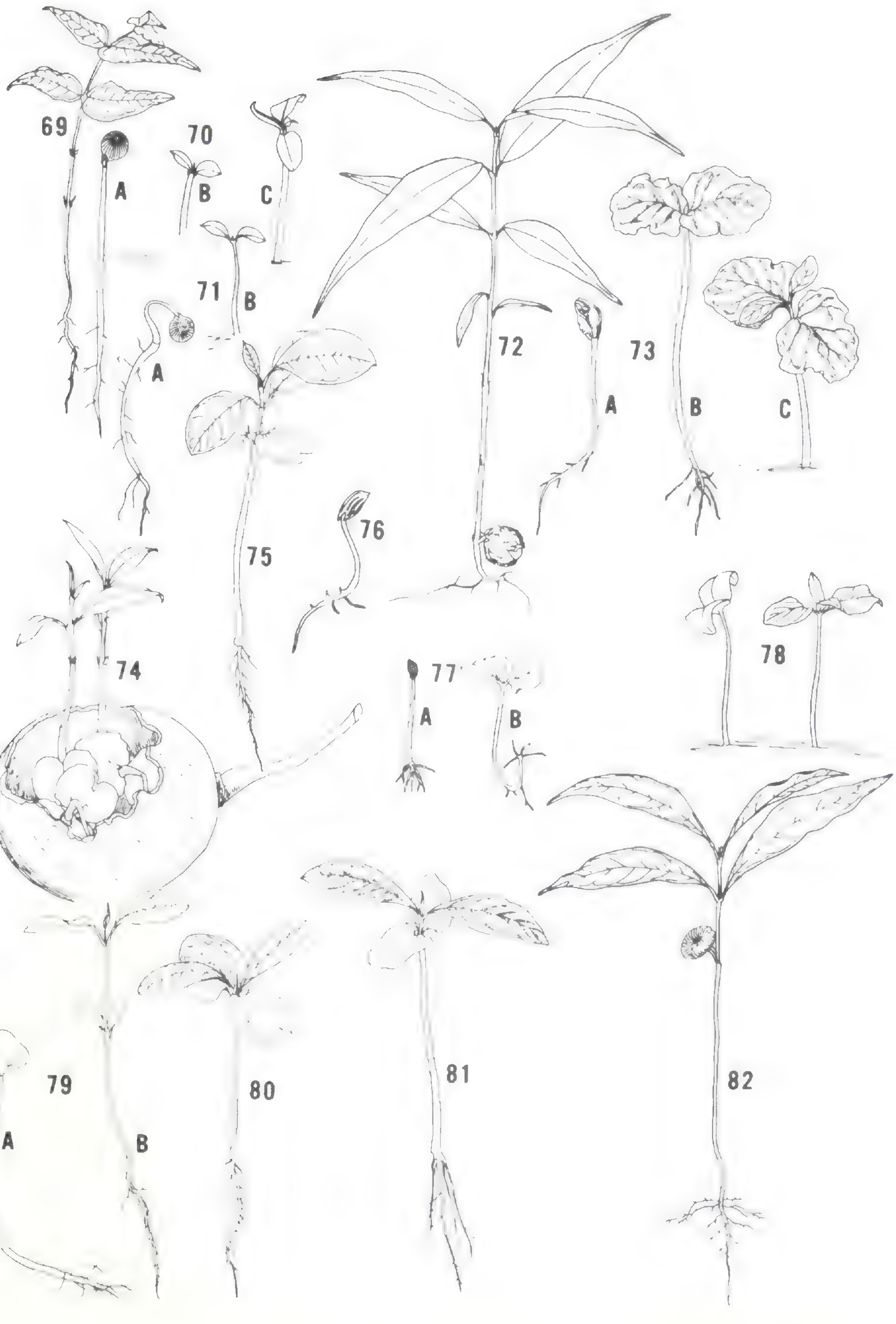

Fig. 69-82. *Mouriri parvifolia* (× 0.4). Fig. 70. *Ardisia* sp. (*Duke 14989;* × 0.4). Fig. 71. *Ardisia* sp. (*Duke 15132;* × 0.4). Fig. 72. *Lacmellea edulis* (× 0.4). Fig. 73. *Stemmadenia* sp. (*Duke 13161;* × 0.4). Fig. 74. *Enallagma latifolia* (× 0.4). Fig. 75. *Crescentia cujete* (*Blume* 3656; × 0.4). Fig. 76. *Coussarea cerrojefensis* (× 0.4). Fig. 77. *Pentagonia* sp. (× 0.4). Fig. 78. *Cephaelis correae* (*Duke 15010;* × 0.8). Fig. 79. *Tocoyena pittieri* (× 0.4). Fig. 80. *Alibertia edulis* (*Blume* 3734; × 0.6). Fig. 81. *Borojoa* sp. (*Bristan 140;* × 0.4). Fig. 82. *Faramea occidentalis* (× 0.4).

VERBENACEAE: Germination phanerocotylar, the cotyledons ovate, entire, subtriplinerved, short-petioled. Eophylls supracotyledonary, opposite, decussate with the cotyledons, often more dentate than the metaphylls. Indument often diagnostic, e.g., the punctate glands in *Tectona* impart a red-spotted outline of the seedling to the newspaper in which it is pressed.

AVICENNIACEAE: Germination phanerocotylar, one cotyledon conduplicate about the other, slightly unequal, broadly reniform, subcordate, sometimes emarginate. Eophylls supracotyledonary, opposite, decussate with the cotyledons, entire, lanceolate to ovate, weakly penninerved.

SOLANACEAE: Germination phanerocotylar, the cotyledons ovoid, penninerved, entire, long-petiolate. Eophylls supracotyledonary, alternate, exstipulate (*Cestrum*).

BIGNONIACEAE: Germination usually phanerocotylar, the cotyledons narrowly to broadly reniform, enervate to plinerved, deeply emarginate to bilobate, cordate to auriculate. Eophylls supracotyledonary, usually opposite and decussate with the cotyledons, simple (in species with simple or digitate metaphylls, e.g., *Crescentia,* Fig. 75), dentate (in species with pinnate metaphylls) or compound (in species with decompound metaphylls).

Enallagma (Fig. 74) is the only cryptocotylar species studied. Note the opposed cataphylls which follow the retuse cotyledons. Although the cotyledons may escape from the testa as it putrifies, they are brownish-black and non-photosynthetic.

RUBIACEAE: Germination usually phanerocotylar, the cotyledons narrowly to broadly ovoid, subplinerved, entire, subsessile to long-petiolate, usually stipulate. Eophylls supracotyledonary, opposite, decussate with the cotyledons, stipulate.

Tocoyena pittieri (Fig. 79) illustrates a fairly common deviation in which the testa (and/or endosperm) is raised characteristically with the cotyledons (cf. also Fig. 76 and 77) which tardily escape to become phanerocotylar. This state is but a step away from true cryptocotyly, as in *Faramea occidentalis* (Fig. 82).

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ADVENTIVE PLANTS NEW TO THE MISSOURI FLORA (III)

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ABSTRACT

Twenty-four taxa (mostly species) are proposed as additions to the adventive flora of Missouri. Of these, 11 are native to the U.S. mostly originating in the South or West, four are European but are already known from the U.S., two are Asiatic, one is from Tropical America and six are escapes from cultivation.

In 1957 and 1960, the author published lists of adventive plants which were collected on the railroads in the City of St. Louis and were new to the Missouri flora. The first list contained 16 plants, and the second 33 (Muehlenbach, 1957, 1960), the great majority of which were species, but in a few cases varieties. J. A. Steyermark (1963) included a further 25 unpublished plants in his *Flora of Missouri*—seven in the text, and another 18 in the supplement. Since that time the writer has found a few more new plants. Omitting all not surely determined plants, the total is 24. Six are escapes from cultivation. Four originate in Europe, but are already known from the U.S., two are Asiatic species, one is considered to come from Tropical America. The remaining 11 plants are native to some area of the U.S., most (at least 8) originating in the South or in the West, and one possibly coming from the Atlantic coast. All plants were sent to specialists for determination or at least for corroboration, as mentioned in the description of each plant. The writer acknowledges with gratitude the help so received. Vouchers for these records (with one exception—*Verbena halei*) have been deposited in the herbarium of the Missouri Botanical Garden. The initials and numbers in parentheses below are those of the writer in field collections.

Eragrostis oxylepis (Torr.) Torr.

One small colony along the fence of the Produce Market at North Market Street, St. Louis Avenue freight yard of the Norfolk and Western Railway (at that time Wabash R.R), October 29, 1961 *(V.M. 1931)*. Determined by G. B. Van Schaack. According to Hitchcock (1951) it is a characteristic southern species (in older literature frequently called *E. secundiflora* Presl.). It is distributed through almost all states from Fla. to Calif. Even though it is found in four neighboring states (Tenn., Ark., Okla., Kans.) one would hesitate to consider this grass a native to Missouri. Too many typical adventives were found in its vicinity, and it also disappeared the following year, although no signs of any threat to the vegetation could be detected. All this suggests that *E. oxylepis* is an adventive plant in this case, since so many of these plants do disappear after one season without any obvious reason.

ANN. MISSOURI BOT. GARD. **56**(2): 163-171, 1969.

Juncus gerardi Loisel.

Two almost confluent colonies in the southern (now abandoned) part of the Ranken yard of the Terminal R.R. Association, east of Compton Ave., June 14, 1964; June 27, July 24, August 29, 1965 *(V.M. 2356, 2476, 2505, 2522)*. Also observed in later years, although a fire heavily damaged the whole vegetation in this locality in the autumn of 1966. Determined by F. J. Hermann. A common plant along the entire Atlantic coast from Me. to Fla., also in Wash. (Jones, 1936), but quite a few times introduced inland. The nearest place is Ind. (Deam, 1940—along R.R.!). Small (1933) adds Great Lake Lowland, Ill. to Mich., but later Jones and Fuller (1955) stated that there is no evidence for the occurrence of *Juncus gerardi* in Ill. Finally Fernald (1950) mentions Minn., Tidestrom (1925) Utah (in Salt Lake City in salt marshes!) and Stevens (1961) N. Dak.

Polygonum pensylvanicum L. var. *rosaeflorum* J. B. S. Norton.

One specimen on the levee of the Mississippi River, between the Eads and Veterans Memorial Bridges, in the vicinity of a Terminal R.R. Association track, September 15, 1963 *(V.M. 2222)*; five specimens on the right-of-way of the Missouri-Pacific R.R., between Davis St. Junction and Tesson St., October 12, 1963 *(V.M. 2275)*; one huge specimen in the Baden freight yard of the Missouri-Kansas-Texas R.R., November 4, 1967 *(V.M. 2914)*. Determined by H. A. Wahl (as were all the other *Polygonum* forms). Gleason and Cronquist (1963) do not mention this variety of the common plant, but Fernald (1950) cites this variety, which he considers a native, in Del., Md. and Va. The status of this variety in Missouri is uncertain. In numerous floras of states between the Atlantic coast and Mo. it is not mentioned, so it could well be an introduced plant for us.

Polygonum lapathifolium L. var. *salicifolium* Sibth.

Few specimens in the now abandoned western part of the Ranken yard of the Terminal R.R. Association, September 7, 1964 *(V.M. 2438a)*; one small colony in the North St. Louis freight yard of the Burlington R.R., August 21, 1966 *(V.M. 2709)*. Gleason and Cronquist (1963) do not mention it at all, but Fernald (1950) cites a number of states, mostly northern, throughout the United States. Generally it is considered a native plant, but St. John (1963) calls it a European weed. However, Hegi (1911, 1957) does not mention it in either edition of his flora.

Polygonum lapathifolium L. var. *prostratum* Wimm.

One specimen on the right-of-way of the Manufacturers Railway, south of Victor St., July 27, 1963 *(V.M. 2150)*. Fernald (1950) gives this description: "shores, railroad-yards and waste places, local, N.S. to Alta. and Wash., s. to N. J., e. Pa. and Calif. (Natzd. from Eu.)" This plant has apparently received little attention, because no other report could be found in the literature consulted.

Polygonum scabrum Moench.

Three specimens in the Inbound freight yard of the Rock Island, Frisco and Chicago and Eastern Illinois R.R., O'Fallon St., October 23, 1966 *(V.M. 2766)*. According to Fernald (1950) the distribution is ". . . New Engl., N.Y., Mich., Minn., Oreg. (Natzd. from Eur.)." Two states more can be added: Ill. (Jones and Fuller, 1955) and Colo. (Harrington, 1964), although the collections are cited under other names. The adventive nature of *P. scabrum* is generally accepted, although Gleason and Cronquist (1963) think that this plant is probably both native and introduced here.

Polygonum persicaria L. forma *albiflora* Millsp.

One colony in Tyler St. freight yard of the Terminal R.R. Association, August 2, 1966 *(V.M. 2695)*; one colony on the right-of-way of the same railroad between Destrehan St. and McKinley Bridge, September 18, 1966 *(V.M. 2731)*. This form of the common *Polygonum persicaria,* naturalized from Europe, seems to be quite frequent too, but in most floras it is mentioned only in the descriptive text of the species without being given a name. Thus Steyermark (1963) in his *Flora of Missouri* wrote, "This annual has pink or dull rose-purplish and green, rarely white flowers." Fernald (1950) mentions the rare forma *albiflora* but does not give any more precise distribution. It is cited in only two of the floras consulted: W. Va. by Strausbaugh and Core (1953) and Minn. by Lakela (1965). H. A. Wahl performed a progeny test (his No. *P875*, coll. July 27, 1967) on *V.M. 2731*. The growth of this test specimen is bigger than the original, and the color of the flowers is pure white.

Beta vulgaris L.

One specimen on the big vacant place adjoining the right-of-way of the Frisco R.R., east of Kingshighway (now completely built over), June 2, 1962 *(V.M. 1963)*. Determined by H. A. Wahl. There are only a few records in the United States for *Beta vulgaris.* As frequently happens with other escaped plants, it has been for the most part overlooked or simply neglected. Only a few floras have apparently tried to register all of them. Especially careful registration of escaped plants has been done in New England. *Beta vulgaris* is cited from four states—Me., N.H., Mass., Conn. (Bean, Hill, and Eaton, 1958). From the other coast, Calif. is mentioned and Munz and Keck (1963) write: "Escaping from gardens and sometimes natur. in low damp places." The root of the St. Louis plant is remarkably thin, so it is not probable that it is a direct garden escape.

Chenopodium watsoni A. Nels.

One specimen in the Carrie Avenue freight yard of the Rock Island R.R., along the car cleaning track, July 1, 1961 *(V.M. 1795)*. Determined by H. A. Wahl. According to him (1954) this species is found in S. Dak., Mont., Colo., N.M., Ariz. and Kans. In connection with the examination of this collection he wrote "An item of particular interest was the collection of *C. watsoni, V.M. 1795,* which is essentially a species of dry areas in the Rocky Mountain region and this is the first collection as an adventive in a weedy habitat" (in litt.).

Atriplex truncata (Torrey) Gray

One small colony in the North St. Louis freight yard of the Burlington R.R., June 30, 1956 *(V.M. 974);* one colony on the right-of-way of the Manufacturers Railway, south of Arsenal St., June 7, 1959 *(V.M. 1521);* possibly on the same place one colony (June 23, July 27, September 15, 1963 *(V.M. 2106, 2147, 2210).* H. A. Wahl expressed his opinion that some of these collections could be *A. truncata.* C. Frankton from the Canada Department of Agriculture in Ottawa confirmed them. He also wrote, "This annual occurs as a native west of 105° Long. in the Northwestern States and Canada. I have not encountered it before as a weedy introduction" (in litt.). It is mentioned in the floras of most western states.

Atriplex heterosperma Bunge.

One colony on the right-of-way of the Terminal R.R. Association east of Geraldine Ave., opposite A.C.L. Haase Co. Food Products plant, July 22, 1956 *(V.M. 1026).* Frankton discovered this species amidst a collection of *A. hastata* L. In a paper with Bassett (1968) he gives the distribution of what has been until now one of the least known adventives in North America. According to them it has spread rapidly in western Canada, especially B.C. in this decade. The first collection was made in 1937. The herbarium of the Canada Department of Agriculture in Ottawa, Ont. also has collections from the U.S.: N. Dak. (Fargo, twice, including what is apparently the oldest collection in the U.S. made by Stevens in 1954) and Wash. (Oroville). Weber (1966) is the only U.S. writer who mentions this plant (Colo., Larimer Co., and Mont., Powell Co., found in both places by G. N. Jones). According to the Canadian paper, *Atriplex heterosperma* is considered to be native to European and Asiatic Russia. It apparently began to spread in the third decade of this century, at first in Europe, then in North America as well, but because of confusion with other species of this genus (especially *A. hastata* L. and *A. nitens* Schkuhr), it was only tardily recognized.

Salsola collina Pall.

One specimen in the southern (now abandoned) part of the Ranken yard of the Terminal R.R. Association, east of Compton Ave., October 4, 1964 *(V.M. 2451b);* several specimens in Tyler St. freight yard of the Terminal R.R. Association, July 17, 1965 *(V.M. 2503).* In both places growing with *Salsola kali* L. *V.M. 2503* was tentatively determined by H. A. Wahl as *Salsola collina.* C. Frankton confirmed this finding, as well as an earlier collection, *V.M. 2451b.* He adds, "We have a sheet from Semipalatinsk which matches your collection very well" (in litt.). This adventive species is quite scarce in the U.S. Pohl and Gillespie (1959) mention Minn. (first discovered 1937 by J. W. Moore), Colo. and Ia. Later this plant was found in N. Dak. (Stevens, 1961). It is a widely distributed Asiatic species, reaching into the southeastern corner of European Russia.

Philadelphus coronarius L.

At least six shrubs over 2 m high on the right-of-way of the Missouri-Pacific R.R. at the crossing with Pennsylvania Ave., along a high stone wall, May 10,

1964, May 28, 1966 *(V.M. 2330, 2614)*. Several more shrubs are growing on the exceedingly steep southern embankment of the same railroad east of Broadway but were not collected since the ground here was very unstable. Determined by D. B. Dunn. *Philadelphus coronarius* is widely cultivated in the U.S. and often escapes. New England reports are available from five states (Me., Vt., Mass., R.I., Conn., Seymour, 1969). Jones and Fuller (1955) and Deam (1940) have encountered it in Ill. and Ind., which is in keeping with the careful search for escapes that has been made in these two states. In addition this shrub has been reported from N.Y. (House, 1924) and Ia. and S. Dak. (Rydberg, 1932).

Prunus armeniaca L.

One small shrub without fruits or flowers. The St. Louis Avenue freight yard of the Norfolk and Western Railway, September 22, 1968 *(V.M. 2987)*. Before the next visit it had been cut down, but in June 1969 some suckers could be detected. Determined by K. Lapins (Pomology Section of Canada Department of Agriculture in Summerland, B.C.). Reported only once as adventive in our range (Gleason and Cronquist, 1963).

Pisum sativum L. var. *sativum* (*P. sativum* L. s. str.).

One small colony with well-developed white flowers in the Bulwer yard of the Terminal R.R. Association, south of the station building of the Carrie Avenue freight yard of the Rock Island R.R., May 8, 1966 *(V.M. 2597)*. Determined by H. Cutler. Like many other garden escapes, peas are very rarely reported. Munz and Keck (1963) mention it as a white-flowering waif from cultivation in Calif. More frequently, the varieties of *Pisum sativum* are not distinguished.

Croton lindheimerianus Scheele.

One small colony on a siding of the Missouri-Pacific R.R., along the National Lead Co. plant west of Macklind Ave., June 2, 1962 *(V.M. 1965)*. Determined by L. H. Shinners. It is a western and southwestern plant. Kearney and Peebles (1960) mention Ariz. (introduced?), Kans. to Tex.; it is reported for Okla. (Stemen and Myers, 1937) and for N.C. (Radford, Ahles, and Bell, 1968).

Parthenocissus tricuspidata (Sieb. & Zucc.) Planch.

One specimen in the now abandoned western part of the Ranken yard of the Terminal R.R. Association, west of Compton Ave., creeping on the ground, August 2, 1964 *(V.M. 2411)*. Determined by D. B. Dunn. One small specimen climbing on the wall of the Frigidaire Warehouse along a siding of the Frisco R.R., east of Kingshighway, May 29, 1965 *(V.M. 2466)*; one specimen climbing on the wall of Ahrens & McCarron building along the Christy Lead of the Missouri-Pacific R.R., north of Beck Ave., May 19, 1968 *(V.M. 2927)*. Determined by W. H. Lewis. In these two localities *Parthenocissus tricuspidata* could be a garden escape, because it was observed on other buildings in the vicinity. In the first locality, however, there are no gardens or houses nearby, and an introduction from outside is possible. Also, it disappeared shortly after the discovery. As with so many other cultivated plants, the reports from other parts of the country are

scanty. Fernald (1950) gives the distribution Mass. to O., and it is included as an escape in Ill. (Jones and Fuller, 1955) and Okla. (Waterfall, 1950).

Gaura sinuata Nutt. ex Ser.

One small but dense colony on the most western track of the Baden freight yard of the Missouri-Kansas-Texas R.R., October 12, 1966 *(V.M. 2760)*. Determined by P. Raven. The area of origin, according to him (in litt.), is Tex. and Okla., and it is introduced sporadically in the Southeast. Further introductions are reported from Calif. (Munz and Keck, 1963) and from N. Y. City (House, 1924). Finally, it is found also in Kans. and Ark. (Rydberg, 1932) and S.C. (Radford, Ahles, and Bell, 1968), but with no judgment as to its status in these states. There is no doubt that *Gaura sinuata* is an adventive in St. Louis. The track where it was found was used intensively in previous years for cleaning the freight cars. Numerous other adventives had grown there, as is often the case in similar places. A little surprising was the fact that the cleaning of the cars was discontinued some years before, and even the track from the freight yard itself disconnected so that no more traffic whatsoever could occur. On the same day another novelty for Mo.—*Physalis acutifolia*—was discovered nearby. The place was visited every summer several times, and it is difficult to understand that two such conspicuous plants could be constantly overlooked for several years. Between this track and the freight yard is a very wide strip of vacant land richly covered with vegetation, and it is not reasonable to assume that both plants represent a recent introduction from the site of the freight yard. During the study of plant introductions, one runs from time to time into puzzles like this which suggest that much more study is needed on distribution mechanisms and factors affecting seed dormancy in wild plants.

Torilis arvensis (Huds.) Link

Right-of-way of Missouri-Pacific R.R., north of Elwood St., June 13, 1954 *(V.M. 151)*; one colony along the northern sidings of the grain elevator of the Missouri-Pacific R.R., south of Steins St., September 2, 1956 *(V.M. 1060)*; one colony in Lindenwood freight yard of the Frisco R.R., east of the R.R. bridge over the Des Peres sewer, July 21, 1962 *(V.M. 1987)*; abundant along a siding of the Manufacturers Railway between its shops and Potomac St., July 15, 1967 *(V.M. 2836)*. *Torilis arvensis* is in all probability the most interesting and perplexing find. On two separate occasions the plants were sent to M. E. Mathias and were identified as *T. arvensis*. This unexpected result suggested a closer examination of the *Torilis* material of the Missouri Botanical Garden. The 23 sheets determined as *Torilis japonica* (Houtt.) DC. from Mo., were all *T. arvensis!* Of 16 sheets from other states, 13 (from nine states) were also found to be *T. arvensis*. Only two sheets (from two states) represent *T. japonica*. In one case no decision was possible. Mathias and Constance (1944) give the characters of the two species: *T. japonica* has an involucre of several bracts, one to each ray, while *T. arvensis* either lacks an involucre, or has a single bract. They also differ in fruit characters. Meanwhile M. E. Mathias informed me (in litt.) that J. T. Howell (1962) found this same confusion to be general throughout studies

of these taxa in the U.S. He cites "frequent misapplication of the name *T. japonica* (*T. anthriscus*) in North America. Whereas most floras of the central, southern and eastern United States refer the loosely branching hedge-parsley to *T. japonica* (or *T. anthriscus*) most of the plants examined (CAS, UCO) belong to *T. arvensis*. *Torilis japonica* (Houtt.) DC. appears to be a rare plant in the United States . . .". Until then *T. arvensis* was listed only from Calif. and Ore. The Californian herbarium material increased the number of states to 11, leaving only three states with proven *T. japonica*. The herbarium material of the Missouri Botanical Garden increases the *Torilis arvensis* states by three (Ala. and Va. besides Mo.), and the *Torilis japonica* states by one, Ind. G. Hegi underlines that both species, which have quite distinct geographical distributions, were frequently confused even in Europe. Apparently this paper of Howell has not received the attention it deserves. In some newer floras no reference to this controversy is given. The only exception seems to be Radford, Ahles, and Bell (1968) in their flora of the Carolinas, but in their preliminary guide (1964) even they considered *T. arvensis* and *T. japonica* as synonyms. Now that *T. arvensis* is known to be quite frequent on the R.R. in St. Louis, the question remains whether *T. japonica* will also be found.

Asclepias subverticillata (Gray) Vail

One big colony spread on several sidings of the Burlington R.R. south of Destrehan St., July 28, 1962, July 28, 1963 *(V.M. 2000, 2152)*. Still present in the summer of 1969. Determined by the late R. E. Woodson, Jr. In his monograph (Woodson, 1954) he gives the range of this western species as Ariz., Colo., Ida., N.M., Tex. and Utah. Kearney and Peebles (1960) added Kans. Kearney and Peebles emphasize that this plant is very poisonous to livestock and "should be eradicated from pastures whenever practicable." At its locality in St. Louis it can not create any danger. One thing was striking, namely the extreme viability. The tracks were frequently treated with weed killers, and once the whole dried vegetation was burned down to the bare ground, but the colony flourished again, as though nothing had happened. Most probably adventive in Mo.

Ipomoea purpurea (L.) Roth var. *diversifolia* (Lindl.) O'Donell

Right-of-way of the Missouri-Pacific R.R. between Reilly Ave. and the signal box at the Davis St. Junction, September 25, 1955 *(V.M. 811)*, October 14, 1961 *(V.M. 1912)*, probably both collections are from one locality. Determined by W. H. Lewis. It seems to be a very rare plant. In the floras consulted *Ipomoea purpurea* with 3-lobed leaves is mentioned only by Gleason and Cronquist (1963) without any further discussion, and by Deam (1940), who found it twice in Ind. No name was given for this variety by either of these authors. O'Donell (1953) has studied *Ipomoea purpurea* var. *diversifolia* in material from N.M., Tex. and Ariz.

Verbena halei Small.

One specimen in the Carrie Avenue freight yard of the Rock Island R.R., July 4, 1957 *(V.M. 1256)*; two specimens in the St. Louis Avenue freight yard

of the Norfolk and Western Railway, June 28, 1958 (*V.M. 1423*); at the same place four plants (only two collected) May 22, 1960 (*V.M. 1607*). Determined by H. N. Moldenke. According to him (1963) this species is wide-spread in the southern states from N.C. to Ariz. Collected also in two neighboring states—Ark. and Okla. In the first mentioned state the nearest point to St. Louis is Stone County, but Moldenke's opinion (in lit.) is that these findings represent accidental introductions.

Physalis acutifolia (Miers) Sandw. (*P. wrightii* Gray)

One specimen in the same locality in the Baden freight yard of the Missouri-Kansas-Texas R.R. as *Gaura sinuata,* and discussed there, October 12, 1966 (*V.M. 2759*). Determined by W. G. D'Arcy. Waterfall (1958) cites this plant under *Physalis wrightii* from Ariz., Calif. and Tex. in the U.S. Later (1967), he used an older name, *P. acutifolia.* Two states could be added: N.M. (Wooton and Standley, 1915) and Colo. (Munz and Keck, 1963).

Cucumis sativus L.

One specimen in the Carrie Avenue freight yard of the Rock Island R.R., on the edge of the roadway separating it from the Bulwer yard of the Terminal R.R. Association, September 9, 1961 (*V.M. 1847*). Determined by H. Cutler. As with other garden escapes, few records are known from other states. Gleason (1952) and Fernald (1950) speak in general terms: "frequently spontaneous in waste ground" or "incline to appear spontaneously." Only Ill. (Jones and Fuller, 1955) has a concrete report. In spite of the dangerous locality, the plant had escaped injuries and even formed edible cucumbers.

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NOTES ON THE GALAPAGOS EUPHORBIEAE (EUPHORBIACEAE)

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ABSTRACT

The tribe is represented by 11 species in two genera, nine of which (eight species of *Chamaesyce* and the only *Euphorbia*) are endemic. A novelty, *Chamaesyce abdita*, is described, and a key furnished to the species of this genus.

The morphological diversity found in the Linnaean genus *Euphorbia* has suggested to a number of workers that the 1500 or more species might well be divided into several, more homogeneous, groups. The element segregated as the genus *Chamaesyce* S. F. Gray appears to be natural and relatively well defined, and has been accepted as distinct in describing this tribe for the *Flora of the Galápagos Islands* (Wiggins & Porter, Stanford University Press, in press). This necessitates several new combinations, and recent collections have included one that must be described as a new species.

Eight of the ten species of *Chamaesyce* found are endemic. They share a number of characteristics, and for the most part are rather distinct from other New World species. Several of them are shrubs and even the herbs have a strong tendency to woodiness at the base or are perennial by their rootstock. In many cases the stems are somewhat swollen at the nodes and pseudoarticulate. Most have a somewhat coriaceous texture, short-petiolate leaves, a reduced number of staminate flowers in each cyathium, and cyathial glands which are dark-colored (at least after drying). The amount of infra-specific variation is high (as seems to be the case throughout the genus), but there is not much overlap in general appearance of the species. (Figures 1 and 2).

The other two species which occur are *Chamaesyce ophthalmica* (Pers.) Burch, a common but rather patchily distributed weed of the American tropics, and *C. hirta* (L.) Millsp., a pan-tropical weed. The two species often grow in mixed stands elsewhere in the New World, with *C. hirta* by far the more aggressive of the two, but this is not the case in the Galápagos where *C. hirta* is known from only one collection.

KEY TO SPECIES OF CHAMAESYCE

1. Capsule glabrous.
   2. Leaves linear, mature stems leafless with leaves clustered on short spurs. . . . . 1. *C. viminalis*
2. Leaves linear-lanceolate or broader, leaves mostly on laterals when stems mature but internodes not condensed to form spurs.
   3. Base of leaf blades deeply cordate enveloping stem, blades orbicular; seed plump, obscurely angled, ca 1.2 mm long, faces smooth . . . . 2. *C. amplexicaulis*

[1] Work on the genus *Chamaesyce* supported by National Science Foundation Grant No. GB-5778 (Principal Investigator Derek Burch).

3. Base of blades at most cordate and scarcely extending over stem, blades elliptic or narrower; seed strongly angled, faces flat, variously sculptured or, if smooth, seed < 1 mm long.
   4. Leaves linear-lanceolate; faces of seed irregular with broken, ± transverse ridges ..... 3. *C. punctulata*
   4. Leaves elliptic; faces of seed smooth or with unbroken transverse ridges.
      5. Stipules ca 1 mm long, bifid or with lacerate margins; cyathial gland appendage merely a light rim to gland; seed > 1.2 mm long, faces with broad transverse ridges ..... 4. *C. recurva*
      5. Stipules ca 0.5 mm long, lacerate to base; gland appendage prominent, to twice width of gland; seed < 1 mm long, faces smooth ..... 5. *C. bindloensis*

1. Capsule pubescent.
   6. Cyathia rather few, not grouped in dense glomerules.
      7. Leaves narrowly elliptic to linear, 12-25 mm long; plants tomentose throughout; faces of seed with fine reticulate markings ..... 6. *C. galapageia*
      7. Leaves ovoid to suborbicular or, if elliptic, < 10 mm long; plants hirsute or strigose throughout; faces of seed essentially smooth.
         8. Seeds plump, obscurely angled; leaf blades broadly ovoid to suborbicular with a cordate base; plants hirsute throughout.. 7. *C. nummularia*
         8. Seeds strongly angled, faces flat; leaf blades elliptic with base oblique; plants strigose throughout ..... 8. *C. abdita*
   6. Cyathia many, collected into dense glomerules.
      9. Glomerules terminal on main axes (often in pairs) or on leafy laterals. ..... 9. *C. ophthalmica*
      9. Glomerules axillary on short leafless peduncles or terminal ..... 10. *C. hirta*

1. *Chamaesyce* **viminea** (Hook. f.) Burch, comb. nov., based on *Euphorbia viminea* Hook. f., Trans. Linn. Soc., London **20:** 184, 1847. Type: Albemarle Island, *Macrae s.n.* (K).—Fig. 1a.

E. viminea f. *albemarlensis* Robinson & Greenm., Amer. Jour. Sci. 3rd ser. **50:** 138, 1895. Syntypes: Albemarle Island, *Macrae s.n.* (K); *Baur 251* (GH), 252 (GH).
E. viminea f. *jacobensis* Robinson & Greenm., loc. cit. Type: James Island, nr Orchilla Bay, *Baur 249* (GH).
E. viminea f. *castellana* Robinson & Greenm., loc. cit. Type: Tower Island, *Baur 247* (GH).
E. viminea f. *chathamensis* Robinson & Greenm., loc. cit. Type: Chatham Island, lower region, SW end, *Baur 245* (GH).
E. viminea f. *carolensis* Robinson & Greenm., op. cit. 139. Type: Charles Island, *Andersson 27* (GH).
E. viminea f. *barringtonensis* Robinson & Greenm., loc. cit. Type: Barrington Island, *Baur 244* (GH).
E. viminea f. *jervensis* Robinson & Greenm., loc. cit. Type: Jervis Island, *Baur 250* (GH).
E. viminea var. *abingdonensis* Robinson & Greenm., loc. cit. Type: Abingdon Island, *Baur 246* (GH).

The variety and forms proposed by Robinson & Greenman can not be distinguished when all the collections now available are assembled. The leaf size, shape, and arrangement, on which their separations were based, are extremely variable even in one collection, and no consistent pattern of variation could be found.

In mature plants the linear leaves are carried on spurs. The collar-like stipules persist after the leaves have fallen.

The capsules are glabrous when young. No mature fruits have been seen, and this might bear some relation to the separation of the sexes that occurs in many

cyathia. Some collections have cyathia with well developed flowers of each sex, but in most cases those with normal-looking female flowers have only tiny males present while those with normal males have only tiny traces of a female. In at least one case both "male" and "female" cyathia occur on the same plant.

Chamaesyce vaginulata (Griseb.) Millsp. of the southern Bahamas is similar in appearance to this species.

2. *Chamaesyce* **amplexicaulis** (Hook. f.) Burch, comb. nov., based on *Euphorbia amplexicaulis* Hook. f., Trans. Linn. Soc., London **20:** 183, 1847. Type: Chatham Island, *Darwin s.n.*, end of Sept. 1835 (K).—Fig. 1b.

In his original description Hooker noted a resemblance between this species and one from the Bahamas. He was probably referring to *C. buxifolia* (Lam.) Small which has similar though larger capsules and smooth plump seeds but does not show the strongly clasping leaf bases, lacerate stipules and black cyathial glands of *C. amplexicaulis*.

3. *Chamaesyce* **punctulata** (Anderss.) Burch, comb. nov., based on *Euphorbia punctulata* Anderss., Stockh. Vet. Akad. Handl. **1853:** 235, 1854. Type: locis sicissimis insulae, Albemarle, *Andersson s.n.* (S — not seen).—Fig. 2a.

Euphorbia diffusa Hook. f., Trans. Linn. Soc., London, **20:** 184, 1847. Type: Albemarle Island, *Macrae & Cuming s.n.* (K). Non Jacquin, Misc. **2:** 311, 1781, nec Dufour, Bull. Soc. Bot. Fr. **7:** 445, 1860.

E. articulata Anderss., Stockh. Vet. Akad. Handl. **1853:** 236, 1854. Type: locis siccis, lapidosis regionis inferioris et mediae insularum Chatham et Indefatigable, *Andersson s.n.* (S — not seen; ? isotype: K). Non Aublet, Hist. Pl. Gui. Fr. 480, 1775.

E. anderssonii Millsp., Publ. Field Mus. Nat. Hist. Bot. Ser. **2:** 63, 1900, based on *E. articulata* Anderss.

The linear-lanceolate leaves, together with the 4-angled irregularly-ridged seed in glabrous capsules, distinguish this species.

The name *E. diffusa* Hook. f. has been widely used for this taxon but is a homonym and illegitimate. Since Andersson's epithet *punctulata* is available it seems better to transfer this rather than trying to justify the retention of the well-known epithet.

4. *Chamaesyce* **recurva** (Hook. f.) Burch, comb. nov., based on *Euphorbia recurva* Hook. f., Trans. Linn. Soc., London **20:** 182, 1847. Type: Chatham Island, *Darwin s.n.*, end of Sept. 1835 (K).—Fig. 1c.

E. apiculata Anderss., Stockh. Vet. Akad. Handl. **1853:** 234, 1854. Type: supra lapides juxta litora insulae Chatham, *Andersson s.n.* (S — not seen).

E. flabellaris Anderss. ex Boiss. in DC., Prodr. **15**(2): 17, 1862. Type: Insula Indefatigable, *Andersson s.n.* (S — not seen).

E. nesiotica Robinson, Proc. Amer. Acad. **38:** 167, 1902. Type: Seymour Island, South, *Snodgrass & Heller* 589 (GH).

The overall appearance, habit and leaf characters are extremely variable in this species. Extremes are well-marked and are the basis for most of taxa here placed in synonymy. There are many intermediates, however, and since such characters as stipule and seed shape (which are usually conservative) are rather constant it seems wiser to treat them as part of a single variable species.

Fig. 1. *Chamaesyce* of the Galapagos. A, *C. viminea* (Hook. f.) Burch. Habit (× 1); B, *C. amplexicaulis* (Hook. f.) Burch. Habit (× 1); C, *C. recurva* (Hook. f.) Burch. Habit (× 1); D, *C. galapageia* (Robinson & Greenman) Burch. Habit (× 1). A after *Wiggins & Porter 340* (MO); B after *Wiggins & Porter 308* (CAS); C after *Snodgrass & Heller 383* (GH); D after *Stewart 1889* (DS).

5. *Chamaesyce* **bindloensis** (Stewart) Burch, comb. et stat. nov., based on *Euphorbia articulata* Anderss. var. *bindloensis* Stewart, Proc. Cal. Acad. Sci. 4th ser. **1**: 91, 1911. Type: Bindloe Island, low shrubs in tufaceous soil in the vicinity of the shore, *Stewart 1868* (GH).—Fig. 2c.

6. *Chamaesyce* **galapageia** (Robinson & Greenman) Burch, comb. nov., based on *Euphorbia galapageia* Robinson & Greenman, Amer. Jour. Sci. 3rd ser. **50:** 144, 1895. Type: Charles Island, June 1891, *Baur 261* (GH).—Fig. 1d.

Euphorbia stevensii Stewart, Proc. Cal. Acad. Sci. 4th ser. **1:** 92, 1911. Type: Albemarle Island, Iguana Cove, *Stewart 1890* (GH, photo DS).

This and the preceding two species have elliptic leaves and are much more similar in overall appearance to other New World species than are most of the endemic species. In particular *C. galapageia* suggests the group, including *C. nutans* (Lag.) Small and *C. hyssopifolia* (L.) Small, with cyathia in more or less dense clusters made up of dichotomising laterals. None of the species in this group show the extreme reduction from this situation that is found in *C. galapageia* and all three of the endemic species differ in seed, cyathia and pubescence characters.

7. *Chamaesyce* **nummularia** (Hook. f.) Burch, comb. nov., based on *Euphorbia nummularia* Hook. f., Trans. Linn. Soc., London **20:** 183, 1847. Type: Chatham Island, *Darwin s.n.* (K).—Fig. 2b.

A distinctive species with small, hirsute, suborbicular leaves, and seeds with face smooth and so plump as to obscure the angles.

Robinson & Greenman described *Euphorbia nummularia* var. *glabra* based on a collection from Floreana (*Baur 386*, GH) (Amer. Jour. Sci. 3rd ser. **50:** 144, 1895). The plants are completely glabrous and have very distinctive, 2-3-lobed leaves with a deep sinus between the unequal lobes. It is much more similar to *Chamaesyce nummularia* than to any other New World species, but I should prefer to see more collections from the island before making a final judgment on its status.

8. *Chamaesyce* **abdita** Burch, sp. nov.—Fig. 2d-g.

Herba prostrata perennis ex caudice ut videtur; omnes partes minutae, strigosae sparsim. *Folia* elliptica, integra; stipulae junctae vel distinctae, integra. *Cyathia* solitaria; glandes stipitatae parum, atropurpurae, appendices obsoletae; flores masculini 3-7 per cyathium. *Semen* anguste ovoideum, 4-angulare, superficiebus plus minusve planis, laeve.

Herb, somewhat woody at base, apparently perennial from the rootstock; stems numerous to 1 mm diam. branching freely from base, the nodes somewhat enlarged, prostrate, to ca 1 cm, sparsely strigose. *Leaves* membranous; stipules joined or distinct, entire, to ca 0.3 mm long; blade elliptic, 1.5-3.5 x 1-1.5 mm, the base oblique, the margin entire, the apex obtuse, sparsely strigose, particularly on lower surface. *Cythia* solitary; glands small, somewhat stipitate, deep purple, appendages obsolete; male flowers 3-7 per cyathium; styles joined at base, bifid and somewhat clavate for ⅓ length. *Capsule* broadly ovoid, strigose, to 1.2 mm long, 1.5 mm wide; seed narrowly ovoid, 4-angled, to 0.7 mm long, 0.5 mm wide, the faces flat, smooth.

Type: Galápagos Islands: Santa Fé: grassy slopes among *Opuntia* and *Bursera,* plateau about 2 km from landing beach at NE of island, alt ca 40-50 m, *Wiggins & Porter 584* (holotype: MO; isotypes: CAS, USF).

Fig. 2. *Chamaesyce* of the Galapagos. A, *C. punctulata* (Anderss.) Burch. Habit (× 1); B, *C. nummularia* (Hook. f.) Burch. Habit (× 1); C, *C. bindloensis* (Stewart) Burch. Habit (× 1); D-G, *C. abdita* Burch. D, habit (× 1); E, leaf bases & stipules (× 2.5); F, cyathium & capsule (× 7); G, seed (× 12). A after *Wiggins & Porter 730* (MO); *B* after *Snow 231* (DS); C after *Wiggins & Porter 300* (CAS); D-G after *Wiggins & Porter 584* (MO).

This tiny species is known only from the type collection, and has perhaps been overlooked by other collectors because of its size. It has some resemblance to *Chamaesyce micromera* (Boiss. ex Engelm.) Wooton & Standley, a North American species also reported from Peru, but differs in pubescence, style length, seed size and smoothness of seed coat. The characters distinguishing it from *C. nummularia* are noted in the key.

Only one *Euphorbia* is known, *E. equisetiformis* Stewart, and this from a single collection. From the rather sparse material available it is difficult to place it in relation to the rest of the genus. The articulate stems and whorled scales or leaves suggest Boissier's section *Alectoroctonum* but it does not appear to be close to other species of this group.

The representation of the remainder of the tribe is extremely poor, and even the weedy species of *Poinsettia* are apparently absent. Their failure to invade the areas disturbed by man is as remarkable as is the lack of success in the colonisation by *Chamaesyce hirta.*

THE GENUS CIENFUEGOSIA CAV. (MALVACEAE)

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ABSTRACT

One novelty, *Cienfuegosia rosei,* is included in the 24 species recognized in this taxonomic revision of the genus. A new subgeneric classification is presented, with two subgenera and seven sections.

INTRODUCTION AND HISTORICAL ACCOUNT

Cienfuegosia is a member of the tribe *Gossypieae* of the *Malvaceae.* Some authors have placed these plants (tribe *Hibisceae* sens. lat.) in the *Bombacaceae,* but the evidence now suggests that they are better retained in the *Malvaceae* (Fryxell, 1968).

The genera included in the *Gossypieae,* in addition to *Cienfuegosia,* are *Gossypium* L., *Thespesia* Corr., *Gossypioides* Skov. ex Hutch., *Hampea* Schlecht., *Kokia* Lewt., *Cephalohibiscus* Ulbr. and *Lebronnecia* Fosb. The principal unifying features that characterize the members of this tribe and which distinguish them from other genera (especially from the *Hibisceae* sens. str.) are (a) the conduplicate embryos, and (b) the presence of pigment glands distributed to various parts of the plant, together with the presence of certain sesquiterpene-like pigments associated with these glands. These pigments (principally gossypol but also several other chemically related compounds) are apparently unique to the tribe *Gossypieae* (Lukefahr & Fryxell, 1967; Fryxell, 1968).

Various botanists have dealt with species of *Cienfuegosia* since Cavanilles established the genus in 1787.

Garcke (1860) was the first of the few who have dealt comprehensively with the entire genus. Fully two-thirds of the species now known were undescribed in Garcke's time.

Hochreutiner (1902) dealt inclusively with the group, but he simply listed the species known at that time, and indicated synonymy and effected nomenclatural changes. He did not attempt to deal with the classification, distribution, or phylogeny of the group. He accepted a circumscription of the genus that was much broader than is now considered valid.

Ulbrich (1914) also simply listed the species and accepted a similarly broad conception of the genus. Hutchinson (1947) provided a delimitation of the genus with which I am in closer agreement, although his treatment of the individual species is not entirely convincing.

Gürke (in Martius, 1892) considered only the species that occurred in or near Brazil; Robinson (1895) treated only the North American species; Rodrigo (1941, 1948) dealt only with the Argentine species; Hutchinson and Dalziel

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(1928) and Exell and Wild (1961) included only the species from specific regions of Africa.

The present study intends to deal in a comprehensive manner with the description and classification of the genus *Cienfuegosia*.

Cavanilles (1787) first described this genus and named it *Cienfuegosia* in honor of the 16th century Spanish botanist Bernardo Cienfuegos, author of "Historia de las plantas." Two years later, A. L. de Jussieu (1789) shortened the generic name to *Fugosia*, the name under which these plants were most commonly known during the ensuing seventy years. During these seventy years, three other variant spellings of the name were published. Linnaeus (posthumously, under the editorship of P. D. Giseke, 1792) published the variant "*Cienfugiosa*." Another variant was the contraction, *Cienfuegia*, of Willdenow (1800). *Cienfugosia* was published by DeCandolle (1824), an error that was perpetuated recently by Hutchinson (1947).

Although *Fugosia* is best regarded as an etymological variant of *Cienfuegosia* and not as a distinct concept, its orthography has been so greatly altered that combinations with the one name cannot automatically be transferred to the other, but must be handled as distinct combinations.

Garcke (1860) reviewed this history and noted the priority of Cavanilles' name. Consequently he transferred several species to *Cienfuegosia* that had been published under the invalid name *Fugosia*.

Ventenat (1800) published the name *Redutea* for a plant that must now be included in *Cienfuegosia*. Ventenat chose this name in honor of the botanical artist, P. J. Redouté, but intentionally altered the orthography in naming the plant. Ventenat's spelling was used by Persoon (1806), but almost all other subsequent authors have cited the name as *Redoutea* Vent., which is the spelling that Kunth used in publishing *Redoutea* Vent., which is the spelling that Kunth used in publishing *Redoutea tripartita* H.B.K. This error may have been perpetuated partly because Index Kewensis lists the name in this way, as does Willis (1966), who moreover attributes *Redutea* to Persoon.

Buckley (1862) published the genus *Elidurandia* (in honor of the botanist Elias Durand) for a plant that must be held indistinguishable from that which Gray (1852) had previously described as a species of *Fugosia*. The name *Elidurandia texana* Buckl. has never achieved currency beyond the original publication and in subsequent citations of synonymy, presumably because Gray (1863) early published his view that the two plants were the same. (Although Shinners (1962, note 5) attempts to defend Buckley against Gray, Gray was certainly correct in this instance.)

RELATIONSHIPS OF THE GENUS

Recently Fryxell (1968) presented a key, distinguishing *Cienfuegosia* from other genera of the *Gossypieae*. There is sufficient variability among the species of *Cienfuegosia* that a combination of characters is generally required to separate it from the other genera. Chromosome number appears to distinguish *Cienfuegosia* (for which $n = 10$ or 11) clearly from the other genera (for which $n = 12$ or

13); but counts are not yet known for the two monotypic genera *Cephalohibiscus* and *Lebronnecia*.

Plant habit also serves to distinguish *Cienfuegosia* from other members of the tribe. *Cienfuegosia* varies from the relatively robust shrub, *C. affinis*, to procumbent herbs such as *C. argentina*. Arboreal forms never occur in *Cienfuegosia*. By contrast *Thespesia, Hampea, Cephalohibiscus, Lebronnecia,* and *Kokia* are typically arborescent (and occasionally shrubby); *Gossypium* and *Gossypioides* are typically shrubby (or occasionally arborescent in the former genus). None of the genera of *Gossypieae* other than *Cienfuegosia* includes herbaceous plants.

A few additional characters merit brief comment. Lewton (1925) discussed the unsatisfactory nature of the number of cells in the capsule as a character for distinguishing genera. Cell number is constant for some genera (three in *Hampea, Kokia,* and *Lebronnecia;* five in *Cephalohibiscus*), but varies from three to five among the species of *Cienfuegosia, Gossypium, Gossypioides,* and *Thespesia*. It is often useful in delimiting lower taxa, however.

The presence of an involucel is characteristic of most plants of the *Gossypieae*. The number of parts of the involucel is of value in classifying these plants at both the generic and specific levels. The genera *Gossypium, Gossypioides, Hampea, Cephalohibiscus, Lebronnecia,* and *Kokia* uniformly have involucels of three bractlets. The involucral bractlets of *Thespesia* and *Cienfuegosia* are more variable, ranging from none (in *Cienfuegosia* sect. *Friesia*) to as many as 20 (in *Thespesia multibracteata* Borss.); but within these genera the number and disposition of bractlets are of taxonomic significance. Attempts to use the form of the bracts as a diagnostic character have not succeeded (Lewton, 1925). The bracts are often caducous in *Thespesia* and in two species of *Gossypium,* but are persistent in the remainder of the tribe.

Involucral nectaries are found in threes at the summit of the pedicel directly below the point of insertion of the involucral bracts. (An additional set of three may also occur, alternate with and above the bracts, in the cultivated species of *Gossypium*.) These nectaries are characteristic of the tribe *Gossypieae,* although they do not occur in all of the species. They are absent in the *Hibisceae* sens. str., although species of *Hibiscus* sect. *Furcaria* have nectaries located directly on the calyx (cf. Janda, 1937). The presence or absence of involucral nectaries is useful in delimiting lower taxa.

The gametic chromosome number in *Thespesia, Hampea,* and *Gossypium* is $n = 13$, with allotetraploidy occurring in *Gossypium*. In *Gossypioides* and *Kokia* the number is $n = 12$. The numbers for *Lebronnecia* and *Cephalohibiscus* are not known. In *Cienfuegosia* numbers of $n = 10$ and 11 have been reported (cf. Table 2).

In addition to the morphological similarities (Fryxell, 1968) that imply phylogenetic relationships, other evidence further substantiates such relationships.

Skovsted (1944) presented evidence from experimental studies with *C. hildebrandtii* that suggests a distant relationship with *Hibiscus*. *Hibiscus rubidus* Skov. and *H. bifurcatus* Cav. set fruit with empty seeds when pollinated by *C. hildebrandtii*. (According to Menzel and Wilson (1961) these two species are

correctly identified as *H. acetosella* Welw. & Hiern. and *H. radiatus* Cav. respectively.) In addition, *C. hildebrandtii* grew vigorously and flowered when grafted onto *Hibiscus esculentus* L. (= *Abelmoschus esculentus* (L.) Moench).

An affinity of *Cienfuegosia* with *Gossypium* is indicated by indirect evidence. One line of evidence concerns the ability of the cotton rust (*Puccinia stakmanii* Presl.) to infect *C. argentina* to a limited extent; this rust fails to infect other species outside of *Gossypium* (cf. Savile, 1954). The cotton rust is an obligate heteroecious rust that alternates between *Gossypium* spp. and *Bouteloua* spp. (Presley and King, 1943; Blank and Leathers, 1963). It occurs in northern Mexico and adjacent parts of Arizona, New Mexico, and Texas. Its primary grass hosts are *Bouteloua aristidoides* (H.B.K.) Griseb. and *B. barbata* Lag., both annuals, though not closely allied. The aecial stage will develop on most species of *Gossypium* (Presley and King, 1943; Blank, personal communication), and can constitute an economic hazard in commercial plantings of cotton in years favorable to rust development. The rust, however, is not known to infect malvaceous plants other than *Gossypium* spp. and *Cienfuegosia argentina.* On *C. argentina* pycnial lesions will form, but these quickly regress and do not develop to the aecial stage.

Attempts to infect other species of *Cienfuegosia* with *Puccinia stakmanii* have given negative results with *C. affinis, C. drummondii, C. sulfurea, C. heterophylla, C. yucatanensis, C. hildebrandtii,* and *C. hearnii* (Blank, unpublished).

It was therefore of interest to discover aecial rust lesions occurring naturally on *Cienfuegosia* in Argentina. Two specimens in the Geneva herbarium (*Rodriguez 12,* of *C. argentina;* and *Monetti 14711,* of *C. hispida*) each show several well-developed aecial lesions. Both were collected in Tucumán in 1913, which may have been a favorable year for the rust in that area.

A request to Ing. M. Gutiérrez (Estación Experimental Agropecuaria, P. R. Sáenz Peña, Chaco) for field observations of rust on *Cienfuegosia* brought a positive response. A. Schulz collected and forwarded for study leaves of *C. ulmifolia* bearing aecial lesions. Schulz observed that 10% of the plants in a natural population in eastern Chaco were infected. Plants of *C. drummondii* and *C. sulfurea* growing in the same area were not infected.

One can conclude, therefore, that a rust endemic to northern Argentina occurs naturally on species of *Cienfuegosia* sect. *Friesia,* and is probably confined to these species. Moreover, the rust is probably a taxon distinct from *Puccinia stakmanii.* This conclusion is substantiated by two facts: (a) *P. stakmanii* infects *C. argentina* incompletely; and (b) rust does not occur in Argentina on the commercial cotton crop (Gutiérrez, personal communication), even though both *Bouteloua aristidoides* and *B. barbata* occur in Argentina. Observations of uredial or telial rust stages on these grasses are at present lacking.

Another line of evidence is given by the host relations of certain insect species that have become pests of cotton and hence of economic importance, particularly those whose host range is relatively narrow. The evidence given by Szumkowski (1952, 1953), Whitcomb & Britton (1953), and Lukefahr & Martin (1962) indicates an affinity of *C. affinis* with *Gossypium,* in that *Alabama argillacea* (Hüb-

ner), *Sacadodes pyralis* Dyar, and *Anthonomus grandis* Boh. are able to develop essentially normally on *C. affinis*.

The red bollworm of cotton, *Diparopsis castanea,* also occurs on *C. hildebrandtii* which is probably its original host (Marshall et al., 1937; Pearson, 1954). *Diparopsis watersi* and *D. tephragramma* occur on *C. digitata* Cav. and *Gossypium anomalum* Wawr. ex Wawr. & Peyr. (Pearson, 1954), but not on *C. heteroclada* (Emsley, 1957).

Finally, the vernacular names of *C. affinis* (see p. 217), all of which may be translated roughly as "wild cotton," and of the Arabian *Cienfuegosia* (Hearn, 1968) indicate an observed resemblance to *Gossypium*.

Ecology

The genus *Cienfuegosia* occurs in a variety of habitats. Yet the general pattern indicates an adaptation to relatively dry or otherwise unfavorable habitats. A few species occur in the severest of xeric environments, notably *C. tripartita, C. chiarugii, C. hearnii, C. rosei,* and *C. welshii.* A few of the more shrubby species are grassland plants; *C. heteroclada* from Nigeria and Ghana is especially adapted to its dry grassland environment because it flowers and fruits directly from the perennial root within a relatively short season (Emsley, 1957), and *C. integrifolia* from Paraguay may be similarly adapted. Many of the South American species occur in chaparral association on sandy soils. Others favor heavy soils. The species of sect. *Friesia* often occur in saline environments. *Cienfuegosia yucatanensis* provides an interesting example in that in Yucatan it occurs on arid, stony soils, while in Florida, Cuba, and Bahama it is found in more mesic environments.

Distribution

Subgenus *Articulata* is African (Fig. 1) and subg. *Cienfuegosia* is American (Figs. 2-5), with the exception of *C. digitata,* which occurs in Africa.

Subgenus *Articulata* is herein divided into three sections: *Articulata; Dioica;* and *Garckea.* Section *Articulata* has a single species, *C. gerrardii,* with a relatively narrow distribution in Natal and the Transvaal. Section *Dioica* also has a single species, *C. heteroclada,* with a restricted distribution from northern Nigeria to northern Ghana. Section *Garckea* has five species, four of which occur around the borders of the Gulf of Aden, the fifth occurring primarily in southeast Africa. None of these species, with the possible exception of *C. hildebrandtii,* is particularly widespread or abundant. The somewhat greater range of *C. hildebrandtii* may result from its probably greater potential for seed dispersal. The distributional pattern of these species does not suggest a precise localization of a "center of origin" for the subgenus.

Subgenus *Cienfuegosia* is divided into four sections: *Cienfuegosia; Robusta; Paraguayana;* and *Friesia.* Section *Cienfuegosia* (Fig. 2) includes six widely scattered species (cf. Fryxell, 1967b), one of which has a disjunct distribution in southern and in northwestern Africa. The other five have discrete and restricted distributions in the following places: Paraguay, Ecuador-Peru, Venezuela, Mexico, and around the Gulf of Mexico (parts of Yucatan, Florida, Bahama, and Cuba).

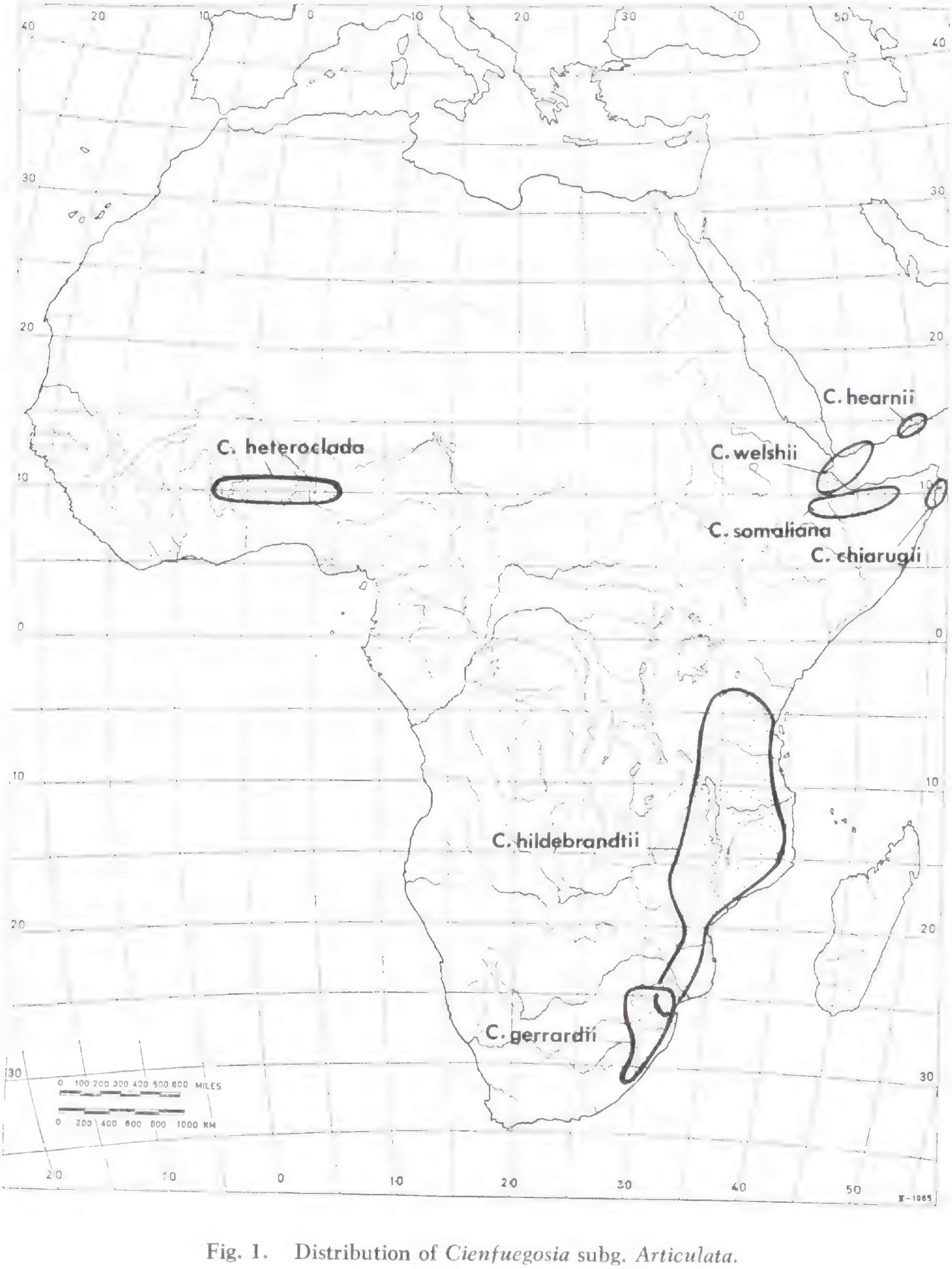
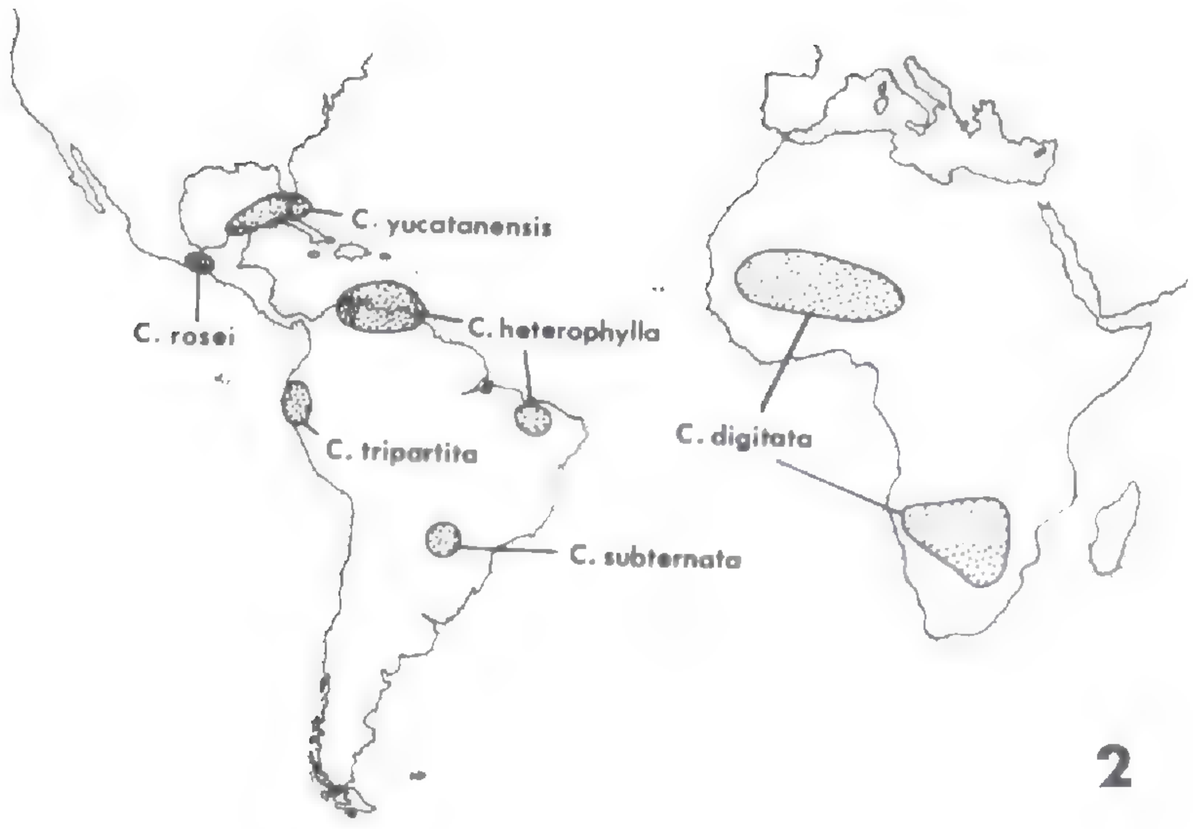


Fig. 1. Distribution of *Cienfuegosia* subg. *Articulata*.

Section *Robusta* (Fig. 3) includes three species, two of which are primarily Brazilian in distribution, extending to Venezuela and Paraguay; the third is Mexican. Section *Paraguayana* (Fig. 4) includes four species that occur in Paraguay and northern Argentina, although one of them, *C. drummondii*, also occurs in southern Texas. Section *Friesia* (Fig. 5) includes four species found primarily in northern Argentina and Paraguay.



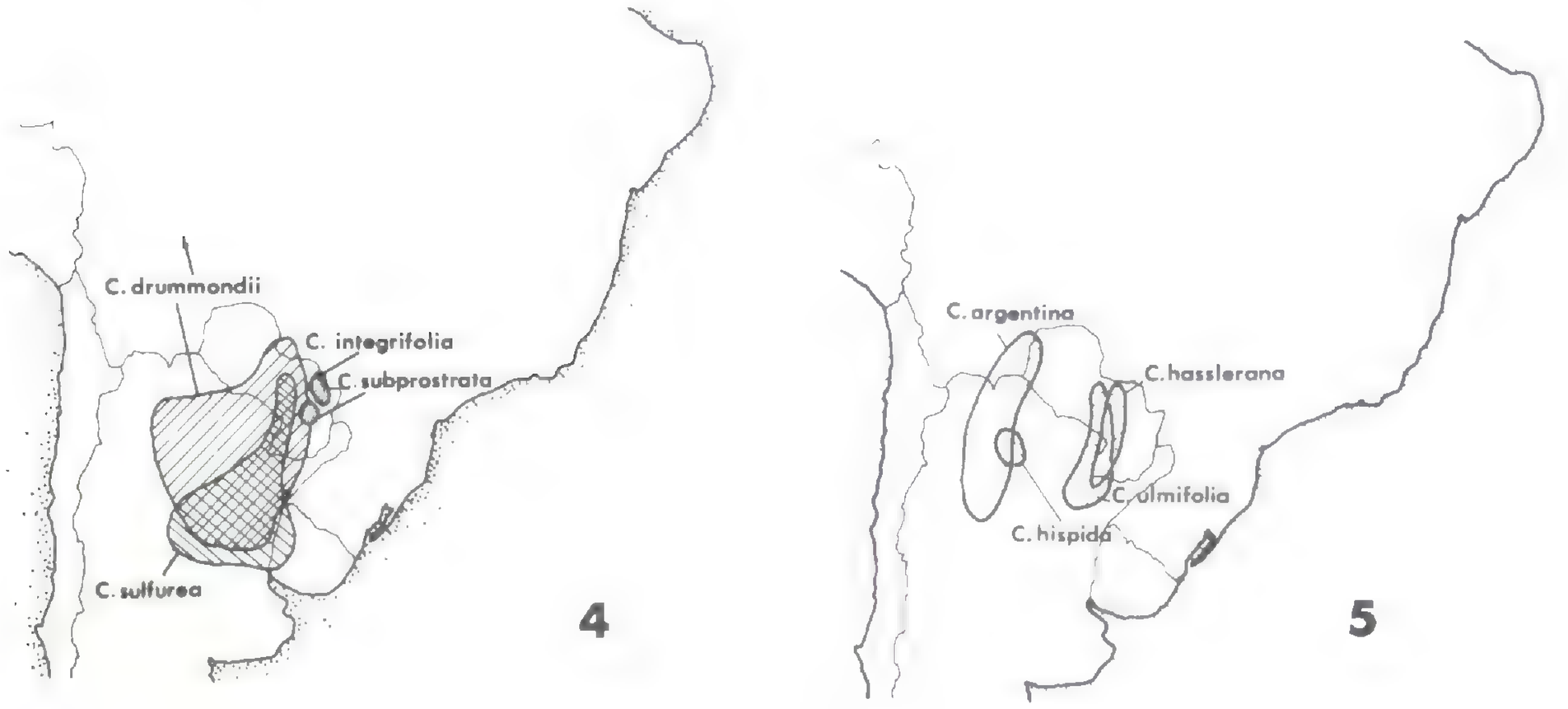


Fig. 2. Distribution of *Cienfuegosia* sect. *Cienfuegosia*. Fig. 3. Distribution of *Cienfuegosia* sect. *Robusta*. Fig. 4. Distribution of *Cienfuegosia* sect. *Paraguayana*. Fig. 5. Distribution of *Cienfuegosia* sect. *Friesia*.

The distribution patterns point to Paraguay as the center of dispersal of the group. Nine species occur within Paraguay, primarily in the southeastern half of the country; three of these are endemic to Paraguay. No other area has comparable diversity.

The general pattern of disjunction previously discussed for *C. drummondii* has been noted for many elements of the American flora; *C. drummondii* was cited as an example in this connection by Bray (1900). This entire question was reviewed by Raven (1963), who concluded that such disjunction of xerophytes probobaly occurred by dispersal from South America to North America in relatively recent time. The distribution of *C. drummondii* accords with this interpretation because: (a) the center of dispersal (or "source") of this group is South American, so that it is more reasonable to suppose that propagules were disseminated from south to north rather than in the opposite direction; and (b) the plants of this species from the two areas are scarcely distinguishable, a factor that suggests

that the disjunction is of relatively recent origin. The only apparent distinction is that the petal spot may be present or absent in the South American specimens but is uniformly absent in the Texas specimens, a variability pattern which further supports the idea of a southern origin.

The distribution of *C. digitata* provides a second example of disjunction in *Cienfuegosia*. The species occurs from southern Angola to the Transvaal in South Africa and from Mauritania to northern Nigeria in northwestern Africa. Hutchinson (1947) stated that the area of the greatest variability of *C. digitata* is in the southern part of its range, and that this is therefore its primary distribution; the more northerly distribution is the result of secondary colonization. I find no such difference in variability. On the basis of the distributional data, implying an American origin and a transatlantic crossing, I prefer the opposite conclusion: that the West African distribution is primary and the South African distribution secondary. The distributional disjunction of *C. digitata* is somewhat parallel with the disjunct distribution of *Gossypium anomalum* in roughly the same areas of Africa, as noted by Pearson (1954) and discussed by Fryxell (1967b). Perhaps those more familiar with the flora of Africa might add additional examples and proffer a phytogeographic interpretation. The lack of morphological divergence between the disjunct populations, both in *C. digitata* and *G. anomalum*, suggests that the disjunction is of relatively recent origin.

The parallel with *G. anomalum* is noteworthy in another way. The other taxa closely allied to *C. digitata* occur in America. Thus, the distribution of the entire group spans the Atlantic. Similarly, taxa closely allied to *G. anomalum* have recently been described from the Cape Verde Islands; this indicates a distributional extension into (if not across) the Atlantic. These distributional data are particularly significant because this species group or its near relatives have been suggested as possible ancestors of the amphidiploid species of *Gossypium* (see Phillips, 1963). The strong distributional parallel that exists between the taxa allied to *C. digitata* and those that are allied to *G. anomalum* may suggest additional clues to the phylogenetic history of *Gossypium*.

The most primitive (as well as the least known) of the six species in sect. *Cienfuegosia* appears to be *C. subternata*, which is endemic to Paraguay. The Ecuadorian-Peruvian *C. tripartita* is apparently derived directly from it. An expansion or migration northward along the Pacific coast of South America is indicated. The Mexican *C. rosei* may be a specialized derivative of this line. The African *C. digitata* and *C. heterophylla* from Colombia, Venezuela, and Brazil, appear to constitute a separate phylogenetic line; this suggests a migration northward along the Atlantic side of South America, and, indeed, across the Atlantic. The insular *C. yucatanensis* is a specialization of *C. heterophylla*. The overall picture indicates an expansion from a center in or near Paraguay northward as far as Yucatan and southern Florida and eastward across the Atlantic. The pattern of distribution of *C. yucatanensis* suggests that it was achieved via salt-water dissemination to coastal and insular sites. Perhaps *C. digitata* was disseminated across the Atlantic by the same means. The transatlantic migration presumably occurred earlier than the African migration that gave rise to the present-day disjunction in the distribution of this taxon.

Reproductive Biology

All species of *Cienfuegosia* are self-compatible, as far as is known, except for the dioecious *C. heteroclada.* Dioecy is confined to this single species in *Cienfuegosia* but is known elsewhere in the *Gossypieae* in *Hampea,* and elsewhere in the *Malvaceae* in *Kydia* and *Napaea.* In subg. *Articulata* self-pollination occurs easily and presumably regularly (except perhaps in *C. gerrardii*) because the decurrent stigma is in close proximity to the androecium. The showy corolla is clearly an adaptation for attracting insects. That cross-pollination also occurs regularly, therefore, seems likely.

In subg. *Cienfuegosia* the basic (primitive) pattern shows a capitate, greatly exserted stigma; thus self-pollination is probably infrequent. This basic pattern has evolved in two directions, both of them involving a reduction in relative style length. The first departure from the basic pattern is found in some species of sect *Cienfuegosia* which have decurrent stigmas similar to those in subg. *Articulata* and in *Gossypium.* The clavate style with decurrent stigmatic lobes that only partially exceed the androecium (expressed in most extreme form in *C. heterophylla*) is clearly an adaptation for increased self-pollination. An overall decrease in flower size accompanies this adaptation.

The second departure from the basic pattern occurs principally in *C. sulfurea* and *C. argentina,* of sect. *Paraguayana* and sect. *Friesia,* respectively. In these species, the upper portions of the style branches are free and partially recurved, so that the stigmatic lobes are brought nearer to the androecium, thus enhancing the possibility of self-pollination. In these same species the petal spot is less prominent, and facultative cleistogamy occurs.

The corolla is bright yellow in all taxa of subg. *Cienfuegosia* (except that it is pale yellow to white in *C. tripartita* and in *C. rosei*). There is a dark spot at the base of each petal in all taxa, except that the spot is small in *C. argentina,* vestigial in *C. sulfurea,* absent in *C. yucatanensis,* and sometimes absent in *C. drummondii.*

Flowering is diurnal in *Cienfuegosia.* The flower generally opens in early morning and withers later in the same day. In some species the flowers close by noon, in others not until late in the afternoon. The corolla, with the androecium attached, falls the next day. Three species, *C. somaliana, C. welshii* and *C. hearnii* (and possibly also *C. chiarugii*) are exceptional in that their flowers do not open until midday, then close later in the afternoon.

Facultative cleistogamy occurs in *C. drummondii, C. sulfurea,* and *C. argentina,* but has not been observed in the other species that are in culture. I tentatively suggest that the phenomenon is confined to the sections *Friesia* and *Paraguayana.* Cleistogamic flowers (which readily produce fruits and seeds) apparently develop in response to environmental factors such as shading. Such flowers are greatly reduced in size (and sometimes number) of parts and have been illustrated by Fryxell (1963). Facultative cleistogamy also occurs in a few species of *Gossypium* and in many species of *Hibiscus* (Fryxell, 1963 and unpublished; F. D. Wilson, personal communication).

The flowers of *Cienfuegosia* are generally campanulate, narrowly so in *C. hearnii.* However, in *C. yucatanensis* the petals flare widely to a fully rotate form.

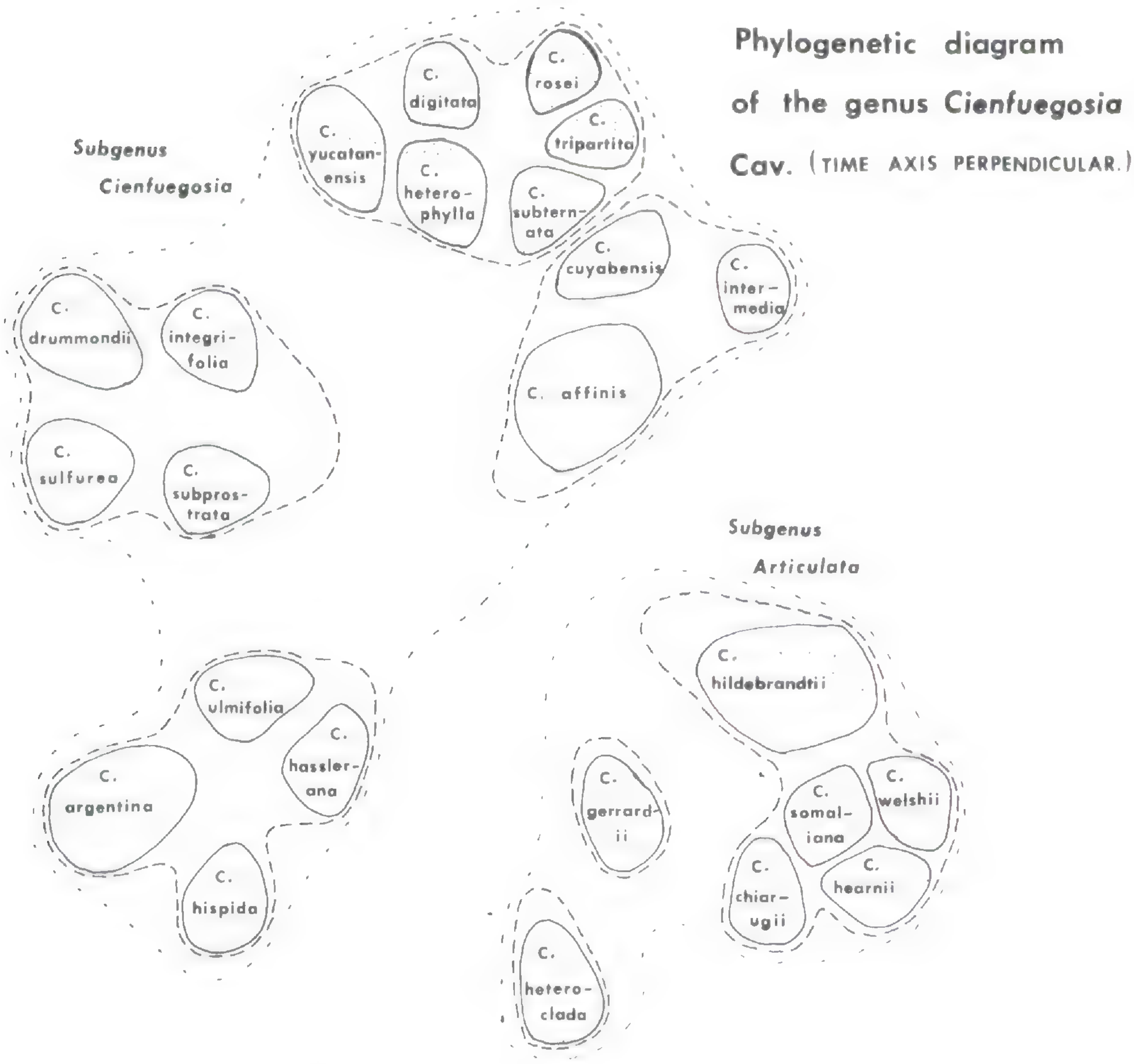


Fig. 6. Phylogenetic diagram of *Cienfuegosia*.

PHYLOGENY

The postulated phylogeny of the genus is illustrated diagrammatically in Fig. 6. Each of the two subgenera of *Cienfuegosia* is considered to be monophyletic, but whether the two groups had a common origin is not clear.

The premises upon which the discussion of specific phylogenetic lines is based appear in Table1.

Table 1. Primitive and advanced traits in *Cienfuegosia* Cav.

Trait	*Primitive*	*Advanced*
Growth habit	Large and shrubby	Small and herbaceous
Pollination adaptations	Outbreeding	Inbreeding
Petal spot	Present	Absent
Stigma	Exserted from androecium	Included in androecium
Flowering branches	Complex	Reduced
Capsule	Pubescent	Glabrous
Pigment glands	Extended to all parts	Restricted to certain parts
Number of seeds per locule	Many	Few

In subg. *Articulata, C. gerrardii* from South Africa is the most primitive representative, as indicated by: its large size and shrubby growth habit; its many-jointed fruiting branches; its more widely distributed pigment glands; and its flower structure that favors outbreeding. Hutchinson (1959) drew attention to the phylogenetic position of this species. (Although it has many primitive traits, *C. gerrardii* exhibits an advanced character in its reduced seed number.) The more complex fruiting branches of *C. gerrardii* have become reduced in two distinct evolutionary lines, while remaining articulated and sometimes several-flowered. One line is represented by the highly specialized *C. heteroclada,* occurring in northern Nigeria and Ghana, which develops many-flowered racemes. The other line includes the shrubby *C. hildebrandtii* from eastern and southeastern Africa and the subshrubs *C. chiarugii, C. somaliana, C. welshii,* and *C. hearnii* from Somalia, Ethiopia, and Aden. In most of these species the flowers are borne singly on articulated peduncles in the axils of the leaves (sometimes more than one in *C. welshii* and *C. hildebrandtii*). This pattern of two evolutionary lines suggests an expansion from south to north. The amount of divergence among the species of this subgenus, including the development of dioecy in one species, indicates that the group is ancient.

In subg. *Cienfuegosia,* sect. *Robusta* is the most primitive group and *C. affinis* is the most primitive species. It is a large, woody shrub with peduncles that are sometime articulated and even (rarely) several-flowered. The flowers are large and clearly adapted to outbreeding, with long styles (nearly equaling the petals) and capitate stigmas. Moreover, *C. affinis* shows the greatest similarity to species of sect. *Articulata,* notably in peduncle articulation and in the more widespread distribution of pigment glands, especially in the corolla. *Cienfuegosia gerrardii* and *C. affinis,* the two species interpreted as the most primitive of their respective subgenera, both have hairy fruits.

Cienfuegosia cuyabensis and *C. intermedia* are intermediate between *C. affinis* and species of sect. *Cienfuegosia* and thus represent transitional forms to or offshoots of this evolutionary line. *Cienfuegosia subternata* is the next step in this series as the most primitive of the six taxa included in sect. *Cienfuegosia.* The distributional and phylogenetic relationships among the six species in this section (noted on p. 183), involve one development that leads to *C. tripartita* and *C. rosei* and another to *C. heterophylla, C. yucatanensis,* and *C. digitata.* Hutchinson (1947) referred to a cline in leaf shape in these species but failed to account for the geographical relations among these plants.

The flower form of *C. affinis* (including such features as the long style, the large corolla, and the prominent petal spot with its characteristic yellow radii) can be traced to at least one element in each of the other sections of subg. *Cienfuegosia.* These examples are: (1) *C. subternata* of sect. *Cienfuegosia,* as already noted; (2) *C. ulmifolia* of sect. *Friesia;* and (3) *C. subprostrata* of sect. *Paraguayana.* The last named species also shares with *C. affinis* the sericeous vestiture of the fruit that is not found elsewhere in the subgenus. Because of this relationship, these species are considered to be the most primitive representatives of their respective sections. Phylogenetic relationships of sections *Friesia* and *Paraguayana,* however, cannot be clearly inferred.

The four species of sect. *Friesia* are closely allied morphologically and do not exhibit any noteworthy phylogenetic series. *Cienfuegosia ulmifolia* is probably the most primitive representative; *C. hasslerana* is closely related to it; *C. hispida* and *C. argentina* are apparently more highly specialized.

The four species of sect. *Paraguayana* are more divergent among themselves than those of sect. *Friesia; C. subprostrata* and *C. integrifolia* are closely allied and relatively more primitive, while *C. drummondii* and *C. sulfurea* are more specialized. In both of these sections the more primitive species are distributed in or near the proposed center of origin of the subgenus, Paraguay, while the derived species have distributions that extend beyond this center to the south and west.

As in subg. *Articulata,* the great divergence among the species of subg. *Cienfuegosia* indicates that the group is ancient.

CHROMOSOME COUNTS

Previously published information on the chromosome numbers of *Cienfuegosia* is meager, Youngman (1931, p. 54) published a somatic (?) chromosome count of 26 for *C. hildebrandtii,* which is identical to the numbers reported for *Gossypium, Thespesia,* and *Hampea.* However, Skovsted (1935, p. 287) later published a count of $2n = 22$ for the same species, and Palacios and Tiranti (1966) and F. D. Wilson (unpublished) confirmed the latter number.

Longley (1933, p. 224) reported $2n = 20$ for *C. heterophylla.* He described the plant as "*C. heterophylla* (Vent.) Garcke, a species native to the southern part of the United States, . . ." Presumably, his material came from the Florida Keys and in fact represents *C. yucatanensis* Millsp.

Palacios and Tiranti (1966) published values of $n = 10$ for three Argentine species, *C. sulfurea, C. drummondii,* and *C. ulmifolia.*

Living material is available for study of twelve taxa, and additional counts have been made as given in Table 2.

Table 2. Chromosome numbers in *Cienfuegosia.*

Species	*Gametic chromosome number*	*Authority* [1]
C. hildebrandtii Garcke	11	Skovsted (1935); Palacios & Tiranti (1966)
C. welshii (T. Anders.) Garcke	11	Wilson (Unpubl.)
C. hearnii Fryx.	11	Wilson (Unpubl.)
C. somaliana Fryx.	11	Wilson (Unpubl.)
C. digitata Cav.	10	Wilson (1968)
C. heterophylla (Vent.) Garcke	10	Wilson (1968)
C. yucatanensis Millsp.	10	Longley (1933)
C. tripartita (H.B.K.) Garcke	10	Wilson (1968)
C. rosei Fryx.	10	Wilson (Unpubl.)
C. affinis (H.B.K.) Hochr.	10	Wilson (Unpubl.)
C. sulfurea (Juss. in St.-Hil.) Garcke	10	Palacios & Tiranti (1966)
C. drummondii (A. Gray) Lewt.	10	Palacios & Tiranti (1966)
C. argentina Gürke	10	Wilson (Unpubl.)
C. ulmifolia Fryx.	10	Palacios & Tiranti (1966)

[1] The unpublished data of F. D. Wilson cited in this table were graciously provided by Dr. Wilson from a manuscript in preparation dealing with the karyology of *Cienfuegosia.*

Hybridization

Twelve of the twenty-four taxa included in *Cienfuegosia* are currently available in the living state for experimental study. Many interspecific crosses have been attempted in this group in order to assess genetic relationships. The following crosses have been successful:

C. welshii X *C. hearnii*
C. digitata X *C. heterophylla*
C. yucatanensis X *C. heterophylla*
C. yucatanensis X *C. digitata*
C. yucatanensis X *C. tripartita*
C. heterophylla X *C. tripartita*
C. argentina X *C. affinis*
C. sulfurea X *C. drummondii* (lethal as seedlings—Palacios and Tiranti, 1966)

Additional crosses are being made. The results of these experimental studies will be reported elsewhere.

Systematic Treatment

Cienfuegosia Cav., Diss. **3**: 174., *t.* 72., *f.* 2, 1787.
Fugosia Juss., Gen. Pl. 274, 1789, pro syn.
Cienfugiosa Gis., Prael. (Linn.) 471, 1792.
Cienfuegia Willd. in L., Sp. Pl. ed. 4. **3**: 723, 1800.
Redutea Vent., Hort. Cels *t. 11*, 1800.
Redoutea H.B.K., Nov. Gen. Sp. Pl. **5**: 293, 1822.
Cienfugosia DC., Prodr. **1**: 457, 1824.
Elidurandia Buckl., Proc. Acad. Sci. Philadelphia **1861**: 450, 1862.

Perennial herbs or subshrubs (sometimes shrubs) with herbaceous to woody stems arising from a woody rootstock. Stems procumbent (but never repent), lax and ascending, or upright; glabrous to pubescent, commonly angled, usually punctate. Leaves entire or coarsely serrate to variously divided, sometimes deeply and secondarily so; linear, elliptic, cuneiform, reniform, or divided digitately; pubescent to glabrous; sometimes punctate; foliar nectaries present (subg. *Articulata*) or absent (subg. *Cienfuegosia*). Phyllotaxy variable, including 2-, 3- and 5-ranked arrangements. Petioles often canaliculate, glabrous to densely pubescent, often with pubescence confined to distal end. Stipules large and foliaceous (sometimes clasping) to minute and subulate; glabrous to pubescent; caducous or persistent. Peduncles axillary; usually uniflorate although sometimes multiflorate, with or without articulation, trigonal, incrassate above, surmounted by three involucral nectaries or these lacking. Involucel sometimes wanting, but usually present, persistent, and 9-12-foliolate (except reduced to 3-foliolate in *C. heteroclada* and partially so reduced in *C. somaliana*); bractlets minute, subulate (and in 3 groups in subg. *Articulata*) or prominent and linear to spatulate, equaling the calyx. Calyx gamosepalous, 5-lobed, usually punctate, glabrous to densely pubescent, sometimes costulate; lobes long-acuminate to rotund-apiculate. Petals 5, distinct, sometimes punctate, stellate-pubescent without, usually showy, yellow (sometimes nearly white), pink, or purple, with dark basal spot (sometimes lack-

ing); flowers withering in a day, sometimes cleistogamic. Anther mass globose, oblate, elliptic, or obovate; staminal column yellowish or dark red, sometimes punctate; stamens sometimes 5-ranked; anthers unilocular, dark red, orange, or yellow; pollen globose, echinate. Style single, sometimes divided apically, usually elongate so that the stigma exceeds the androecium, sometimes punctate; stigmas 3-5-lobed (or if style divided, stigmas distinct), usually exceeding androecium, decurrent or capitate, dark red or yellowish, sometimes pubescent. Fruit a capsule, usually 3-loculed (sometimes 4-5-loculed), ovoid, globose, sometimes obovoid, or notably elongated (in *C. somaliana* and *C. welshii*), glabrous or weakly to densely ascending-sericeous, usually punctate, sometimes with hairs on inner margin of suture. Seeds 3-8 mm, turbinate, minutely puberulent (in *C. affinis*) to densely comose; hairs tightly appressed (*C. drummondii*), loosely appressed, or patent, light tan to rufous-red, up to 10 mm long. Embryos conduplicate. Cotyledons cuneiform to sub-reniform, obtuse to emarginate, sometimes punctate.

The indumentum is variable; some species are densely pubescent while others are essentially glabrous. Pubescence is generally greater on the under surface of the leaves. Plant hairs (except for those on the seed coat) are usually stellate and vary in size from minute puberulence to hairs 1-2 mm in length. Pubescence is characteristically red-brown in *C. gerrardii*. Where longer hairs occur, they are often reduced from stellate clusters to single, semi-scabrous structures.

Pigment glands are found in all above-ground parts of the plant in a few species and are variably distributed in others. The varying distributional patterns have taxonomic significance, especially in the extension of these glands to the floral parts. The glands are always present on the calyx (except sometimes in *C. hearnii*), although they are often very obscure in species of sect. *Friesia*. Glands of the calyx are especially prominent in sect. *Cienfuegosia*. Hutchinson (1947) described these calyx glands as "confined to a double row along each nerve" and used this as a diagnostic trait to distinguish *Cienfuegosia* from its allied genera, in which he described the calyx glands as "scattered, sometimes absent." Although the calyx glands in *Cienfuegosia* are often oriented in the regular fashion described by Hutchinson (e.g., *C. tripartita*, *C. heteroclada*), they are also quite irregularly placed in certain species (e.g., *C. drummondii*, *C. hildebrandtii*); therefore, it is necessary to reject this trait as diagnostic for the genus. The comparative morphology of the embryos of *Cienfuegosia* spp. (Fryxell, 1968) shows them to bear a marked resemblance to those of *Gossypium*, except that most of the species of *Cienfuegosia* have embryos lacking the dark pigment glands, while only a few of the species of *Gossypium* are lacking them. Type species: *Cienfuegosia digitata* Cav.

ARTIFICIAL KEY TO THE SPECIES OF CIENFUEGOSIA, BASED ON VEGETATIVE CHARACTERS

a. Leaves deeply dissected or compound.
  b. Plants procumbent herbs.
    c. Leaf segments rounded to obovate, crenate ..... 21. *C. argentina*
    cc. Leaf segments linear, dentate ..... 24. *C. hasslerana*
  bb. Plants ascending herbs or subshrubs.
    d. Foliage odoriferous ..... 4. *C. somaliana*
    dd. Foliage non-odoriferous.

e. Leaves trifoliolate ..... 12. *C. subternata*
ee. Leaves not compound.
f. Leaves large, deeply 3-parted (at times trifoliolate) .. 13. *C. tripartita*
ff. Leaves moderate, digitately divided.
g. Leaf lobes acute ..... 8. *C. digitata*
gg. Leaf lobes obtuse ..... 16. *C. intermedia*
aa. Leaves simple or moderately lobed.
h. Leaves simple, entire.
i. Plant hirsute ..... 14. *C. affinis*
ii. Plant glabrate.
j. Foliar nectaries present, apical ..... 7. *C. heteroclada*
jj. Foliar nectaries lacking.
k. Stipules often equaling petioles ..... 19. *C. integrifolia*
kk. Stipules inconspicuous.
l. Leaves orbicular ..... 20. *C. subprostrata*
ll. Leaves otherwise.
m. Leaves 1-2 times as long as broad.
n. Leaves cuneiform to obovate, obtuse ..... 5. *C. chiarugii*
nn. Leaves ovate, apiculate ..... 10. *C. rosei*
mm. Leaves much longer than broad.
o. Leaves 4-10 times as long as broad ..... 9. *C. yucatanensis*
oo. Leaves 2-4 times as long as broad.
p. Leaves elliptic, penninerved ..... 15. *C. cuyabensis*
pp. Leaves ovate, palminerved ..... 11. *C. heterophylla*
hh. Leaves more or less lobed or, if simple, then dentate.
q. Stipules foliaceous.
r. Stipules symmetrical; leaves cordate ..... 1. *C. gerrardii*
rr. Stipules auriculate-clasping; leaves truncate.
s. Plant procumbent herb ..... 23. *C. ulmifolia*
ss. Plant upright subshrub ..... 2. *C. hildebrandtii*
qq. Stipules inconspicuous.
t. Foliage odoriferous.
u. Leaves ciliate-margined ..... 4. *C. somaliana*
uu. Leaves glabrous ..... 6. *C. hearnii*
tt. Foliage non-odoriferous.
v. Plants hirsute.
w. Stipules subulate, symmetrical ..... 17. *C. sulfurea*
ww. Stipules auriculate, asymmetrical ..... 22. *C. hispida*
vv. Plants glabrate or puberulent.
x. Plants procumbent ..... 21. *C. argentina*
xx. Plants ascending.
y. Foliar nectaries present.
z. Petioles shorter than lamina ..... 7. *C. heteroclada*
zz. Petioles longer than lamina ..... 3. *C. welshii*
yy. Foliar nectaries lacking.
A. Leaves simple, dentate ..... 18. *C. drummondii*
AA. Leaves trilobed; lobes entire.
B. Leaf lobes obovate ..... 16. *C. intermedia*
BB. Leaf lobes lanceolate to ovate.
C. Leaves large, deeply & variably lobed .. 13. *C. tripartita*
CC. Leaves moderately sized and lobed.
D. Leaves mostly acute to obtuse .. 11. *C. heterophylla*
DD. Leaves apiculate ..... 10. *C. rosei*

No previous subgeneric classifications have been proposed in *Cienfuegosia,* although Garcke (1860) separated an American and an African group, and Hutchinson (1947) suggested certain species alliances. Neither author, however, gave taxonomic status to these groups or provided them with a nomenclatural basis. The present treatment divides the genus into two subgenera and seven sections.

KEY TO THE SUBGENERA

a. Peduncles articulate (sometimes obscurely so at base); flowers solitary or on several-flowered sympodial branches; petals punctate; stigmas decurrent; foliar nectaries usually present; bractlets of involucel in three groups I. *ARTICULATA* (p. 194)
aa. Peduncles non-articulate; flowers solitary in the leaf axils; petals epunctate (or if peduncles articulate or petals punctate, then stigma capitate); stigmas capitate or decurrent; foliar nectaries lacking; bractlets of involucel not grouped, sometimes lacking . . . . . II. *CIENFUEGOSIA* (p. 204)

I. SUBG. **Articulata** Fryxell, subgen. nov.

Folia punctata, plerumque cum nectariis infra. Pedunculi articulati. Involucrum breve, saepissime 9-phyllum; foliolata involucrorum tribus in turmis disposita. Petala punctata. Stigmata decurrentia.

Leaves of variable form, punctate, with 0-3 dorsal foliar nectaries. Flowers solitary or on several-flowered sympodial branches. Peduncles articulate, bracteate at articulation, surmounted by 3 prominent involucral nectaries. Involucel of 9 bractlets arranged in 3 groups (or these reduced to 3), each group surmounting an involucral nectary (or nectaries absent in sect. *Dioica*); bractlets inconspicuous, triangular or subulate, persistent. Calyx punctate (punctae sometimes restricted in distribution, or lacking); lobes acute or rotund-apiculate. Petal punctate, yellow, purple, or cream-colored with dark spot on claw. Stigmas decurrent, 3-4-lobed. Fruits glabrous or minutely pilose, usually punctate.

Type species: *Cienfuegosia gerrardii* (Harv. ex Harv. & Sond.) Hochr.

The name of this subgenus is chosen in reference to the articulated peduncles that characterize it.

KEY TO SECTIONS OF SUBGENUS ARTICULATA

a. Shrubs; leaves markedly cordate, palmately trilobed, lobes rounded, entire; stipules large, foliose, oblong, sessile; pedicels subtended by foliar leaf . . . 1. *Articulata* (p. 194)
(contains single species: 1. *C. gerrardii*)
aa. Subshrubs or perennial herbs; leaves cuneate, entire or dentate, sometimes shallowly lobed or deeply dissected; stipules triangular, subulate or auriculate; pedicels subtended by small bracts.
b. Leaves cuneiform to flabelliform or reniform, entire, dentate, or dissected; peduncles in axils of leaves, 1-2-flowered; stipules triangular, auriculate or subulate; bractlets of involucel 9 . . . . . 2. *Garckea* (p. 196)
bb. Leaves obovate, entire (sometimes apically tridentate); flowers dimorphic, in short racemes appearing before leaves; stipules subulate; bractlets of involucel 3, irregular . . . . . 3. *Dioica* (p. 203)
(contains single species: 7. *C. heteroclada*)

1. SECT. ARTICULATA

Cienfuegosia subg. *Articulata* Fryx. sect. *Articulata*

Leaves profoundly cordate. Stipules prominent, obtuse, foliaceous. Flowers borne on sympodial fruiting branches. Peduncle articulated, bearing foliar leaf at articulation.

Type species: The type of sect. *Articulata* is the type of subg. *Articulata, C. gerrardii*.

1. *Cienfuegosia gerrardii* (Harv. ex Harv. & Sond.) Hochr., Ann. Cons. & Jard. Bot., Genève **6:** 56, 1902.

Fugosia Gerrardi Harv. ex Harv. & Sond., Fl. Cap. **2**: 588, 1862 [Type: Ladysmith, Natal: *Gerrard 632* (TCD-n.v.)].

Thespesia Rehmannii. Szyszl., Polypet. Thal. Rehmann. 44, 1888 (=Rozpr. Spraw. Posiedzen **17**: 136, 1888) [Type: Ladysmith, *Rehman 7128* (n.v.)].

Illustrations: Fig. 17, d-e; also Wood (1911) t. 563; Janda (1937) Figs. 18, 28, 34; Fryxell (1968) Fig. 3,a.

Branched open shrub; stems upright or lax, weakly ridged to terete, punctate, moderately covered with a minute stellate tomentum having a characteristic red-brown color. Leaves cordate, acute, sub-entire to moderately 3-5-lobed, sparingly pubescent to glabrate, ciliate-margined, 2-3 cm long, usually broader; lobes rotund; foliar nectary single, basal, elongate (1-2 mm). Petioles pubescent, terete, obscurely punctate, about ½ length of lamina. Stipules foliaceous, entire, persistent, elliptic to oblong, obtuse, 1-nerved, cuneate-sessile, pubescent to glabrate, punctate, 1-2 cm long (equaling or exceeding petioles), 3-8 mm broad, symmetrical. Fruiting branches sympodial, several-flowered, articulate and foliate at base of each pedicel. Pedicels ½-1½ cm, puberulent to glabrate, surmounted by 3 large bordered nectaries. Involucel of 9 bractlets in 3 groups; bractlets irregular, subulate (1-3 mm) or occasionally larger (up to 8 mm) and then often spatulate and somewhat foliose, punctate, 1-nerved, glabrate. Calyx 1-1½ cm, costulate, puberulent to glabrate; lobes 3- (rarely 5-) ribbed, triangular, acute (sometimes rounded, sometimes acuminate, rarely 1-toothed), 4-7 mm long. Petals yellow, 2-3½ cm with small dark-red spot on claw (spot sometimes lacking). Anther mass globose to obovoid; filaments 2-4 mm, reddish [in sicco]; androecial column and occasionally the filaments sparingly punctate; anthers red; pollen light-colored. Style markedly punctate, exceeding androecium; stigma 3-lobed. Fruit 3-loculed, globose to obovoid, 1-1½ cm, rostrate, short-pilose without, glabrous within. Seeds one per locule, 8 mm long, 5 mm wide, oval in outline, soft-pubescent; seed hairs dense, brown, ⅓ mm. Embryo punctate.

Distribution (Fig. 7): Transvaal: in the region of Lydenburg and Middleburg; Swaziland; Natal: nearly to the coast, and as far south as the Umzimkulu River; Mozambique: west of Laurenço Marques (Excell and Wild, 1961).

Marshall, Parson, and Hutchinson (1937) note that the ecological distribution of this species in South Africa and Swaziland is confined to the middle veld district, which is defined roughly as the area included within 2000 to 4000 feet elevation. The plant occurs "in colonies growing in scanty soil in the hilly ground above 1400 ft."

SOUTH AFRICA: NATAL: Zululand: *Gerrard 257* (BM); Magul, Ngotsche, *Parsons s.n.*, Dec 1925 (PRE); Port Natal, *Gerrard & McKen. s.n.* (S- this specimen is incorrectly denoted as the type); Camperdown, 2000 ft, *Wood 239* (FE), *11722* (PRE); *Haygarth s.n.*, 1883 (BM). Griqualand East: In clivis pr. "Clydesdale" ad flum. Umzimkulu, 2500 ft, *Tyson 1408* (G, Z). TRANSVAAL: Lydenburg, *Wilms 83* (BM, G, L, M, P, PH), 4800 ft, *Schlechter 3950* (G, M, UC, Z); outside village on Farm Rovidraai, open scrub in riverbank ± 4800 ft, *Liebenberg 3492* (PRE); procumbent on riverbank, 4700 ft, *Galpin 12193* (PRE), *Rogers 14561* (Z); Kruger National Park, Pretoriashap, 2000 ft, *v. d. Schijff 2076* (PRE); Middleburg, *Wilms 83b* (G, L), *Kassner 121* (BR); bei Brankhorst-Spruit, *Wilms 83a* (BM, Z).

SWAZILAND: Bremersdorp, *Hutchinson 5* (PRE).

2. SECT. **Garckea** Fryxell, sect. nov.

Folia cuneiformia vel reniformia, simplicia vel dissecta. Stipulae magnae etiam auriculatae-acuminatae, aut parvae et subulatae. Pedunculi plerumque axillares, articulati, squamis parvulis ad articulos.

Subshrubs. Stems glabrous to pubescent, weakly angular, punctate, often obscurely so. Leaves cuneiform to reniform, entire (except sometimes dissected in *C. somaliana*) or sometimes 3-lobed, dentate- or serrate-margined on upper portion, punctate (sometimes translucently so), glabrous to pubescent. Foliar nectaries 0-3. Petioles glabrous, puberulent, or scabrous, punctate, usually canaliculate. Stipules large and clasping or inconspicuous and subulate. Flowers 1 or 2 (rarely more) on axillary peduncles or short sympodial branches. Peduncles articulate, with much-reduced bract at articulation, surmounted by 3 involucral nectaries. Involucel of 9 bractlets in 3 groups, each group usually surmounting a nectary; bractlets subulate, sometimes laterally connate. Calyx costulate (except in *C. chiarugii*), splitting and pseudo-bilabiate in flower and fruit; lobes rotund-apiculate, 3-5-ribbed. Petals yellow, purple, or cream-colored, with dark claw. Androecium purple or orange; pollen cream-colored or orange. Fruit prominently or obscurely punctate, glabrous to minutely pilose, ovoid to slightly obovoid or greatly elongated. Type species: *Cienfuegosia hildebrandtii* Garcke.

Chiovenda (1929) published *C. chiarugii* and established the section *Synodontos* to include that species, but did not provide a diagnosis for the name. Moreover, he based the section on (and derived its name from) a single trait, a gamophyllous involucel, which *C. chiarugii* does not possess. This name cannot be accepted as valid because the *descriptio generico-specifica* pertains only to monotypic genera (Article 42). Section *Synodontos* is not monotypic and was not considered to be by Chiovenda. It is possible to validate Chiovenda's name by providing the necessary diagnosis, but since the name was descriptively ill-chosen, it is considered preferable to publish a new name not encumbered with a misconception. Such a course is not in violation of Article 62 since the name Synodontos was not validly published.

The name *Garckea* is chosen to honor A. Garcke, who made the first significant evaluation of *Cienfuegosia* (1860) and who later described the type species of this section.

KEY TO SPECIES OF SECTION GARCKEA

a. Stipules prominent, auriculate-clasping; foliar nectaries 3, basal; petals yellow; androecium orange ..... 2. *C. hildebrandtii*
aa. Stipules inconspicuous, subulate; foliar nectaries 1-3, medially positioned, sometimes absent; petals yellow, cream, or purple; androecium purple.
b. Petioles as long as lamina or longer, puberulent or scabrous, especially at distal end; plant puberulent or pubescent (at least on petioles); petals yellow or cream.
c. Leaves reniform, denticulate, sparsely scabrous below and on petiole, nonodoriferous, 5-ranked; foliar nectaries 3; peduncle exceeding leaves, articulated near center; petals cream ..... 3. *C. welshii*
cc. Leaves flabelliform, slightly 3-lobed to deeply dissected, dentate, minutely puberulent on margin and petiole, odoriferous, 3-ranked; foliar nectary 1 (-3 or rarely 0); peduncle shorter than leaves, articulated basally; petals yellow ..... 4. *C. somaliana*

bb. Petioles shorter than the lamina, glabrate; plant essentially glabrous; petals purple.

d. Leaves obovate; calyx ecostulate, prominently punctate; foliar nectaries lacking ..... 5. *C. chiarugii*

dd. Leaves cuneiform, odoriferous; calyx costulate, punctate or epunctate; foliar nectaries 1-3 ..... 6. *C. hearnii*

2. *Cienfuegosia hildebrandtii* Garcke, Eichl. Bot. Jahrb. Bot. Gart. Berl. **2:** 337, 1883 [Holotype: Txamtei in Duruma. Im Gras auf salzigem Boden, *Hildebrandt* 2325 (probably B†). Neotype: Tanzania: Lushoto District: 3 miles NW of Mombo, 29 Apr. 1953, *Drummond & Hemsley* 2285 (BR, isoneotypes: B, FI)].

Illustrations: Fig. 17, a-c; also Marshall, Parson, and Hutchinson (1937) Figs. 1-3; Exell & Wild (1961) t. 85; Fryxell (1968) Fig. 3,b.

Small, branched, upright shrub. Stems usually minutely pubescent, sometimes glabrous, terete. Leaves broader than long, cuneate, flabelliform, unlobed to weakly trilobed, irregularly dentate, 3-nerved, glabrate above, sometimes minutely pubescent below, ciliate-margined. Foliar nectaries 3 (rarely lacking), basal. Petioles about ⅓ length of lamina, densely pubescent throughout to moderately pubescent on upper surface only. Stipules auriculate-clasping, asymmetrical (rarely lanceolate, symmetrical), acuminate, entire, pubescent or glabrate, ciliate-margined, 6-10 mm long (½-⅔ length of petiole) rarely longer, half as broad. Peduncles solitary (rarely multiple), equaling or barely exceeding petiole, articulate and bracteate near center, punctate, often pubescent, nectaries prominent. Involucel bractlets 1-3 mm, central bractlet of each group often exceeding lateral bractlets, rarely partially connate. Calyx 7-10 mm, sparingly punctate (often only at base of tube) to nearly epunctate, costulate, scarious in intercostal areas, glabrous or pubescent; lobes shallow, 3-ribbed, rotund-apiculate. Petals 3-4 cm (rarely smaller), sparingly punctate, yellow with large dark-red spot on claw. Androecial column pallid, punctate; filaments dark-red; anther mass globose; anthers unranked, orange; pollen orange. Style epunctate, exceeding androecium; stigma dark-red, pubescent. Fruit ovoid to obovoid, obscurely punctate, glabrous to weakly pilose, 3-4-loculed, 10-14 mm long. Seeds turbinate, 5-6 mm long, densely comose; hairs 8-10 mm, straight, soft but appearing bristly, red-brown to dirty-tan color. Embryo epunctate, but with reddish punctae developing on mesocotyl and cotyledonary margins upon germination. Chromosome number: $n = 11$.

The variation in vestiture that is characteristic of this species can be noted even on individual collections. For example, both glabrous and pubescent branches occur among the duplicates, even on a single sheet, of *Schlechter 11770* (Z).

Hochreutiner separated two branches of the collection of *Braga* 82 (Z), differing in pubescence, as distinct varieties in manuscript names. I do not believe that a varietal distinction based on pubescence is warranted because: (a) there is no correlated variation in other traits, and (b) there seems to be no geographical basis for the distinction. Therefore, the varietal epithets suggested by Hochreutiner shall herein remain unrecognized.

Distribution (Fig. 8): Natal, Swaziland, and the Transvaal in the south northward along the eastern coast of Africa to central Mozambique. It also occurs in Tanzania, but according to Pearson (1954) is absent between there and central Mozambique. Specimens were cited by Gonçalves (1963) from southern and central Mozambique; Marshall, Parson, and Hutchinson (1937) cited its occurrence in Southern Rhodesia, northern Mozambique, and southern Tanzania, indicating a relatively continuous distribution. These localities are included in the distribution map since there appears to be no question of the identity of the plants concerned. In the southern part of its range, where it overlaps the range of *C. gerrardii,* it is separated ecologically from this species, occurring at lower altitudes. Ulbrich (1914) asserted that *C. hildebrandtii* occurs in Madagascar, but no specimens from there are known to me.

Marshall, Parson, and Hutchinson (1937) gathered important ecological data on the distribution of *C. hildebrandtii,* at least in the southern portion of its range, which Pearson (1954) indicated to be its principal distribution. They found it to occur in close association with *Acacia barbertonensis* Schweick. at altitudes below 1300 feet, to be absent from areas with "thin, stony soils," and to be present in regions of "better and deeper soils." They divided the habitats in which *C. hildebrandtii* occurs into three types: "(a) the crests and sloping sides of low elevations, (b) along water channels, and (c) pans *(vleis).*" (The last named are depressions often characterized by impermeable (saline?) soil, vegetated only on the margins.) They noted that the occurrence of the plant on the water channels and pans is "consequent on proximity to watercourses" and drew particular attention to the dissemination of seeds by water, since their bristly vestiture renders them buoyant.

However, *C. hildebrandtii* occurs primarily on the crests of low hills having good soil cover. Water-borne dissemination does not account for this occurrence. The seeds of this species have bristly hairs that stand straight out, and thus appear to be well-adapted to wind-transport (as a tumbleweed). The seeds drop from the plant very quickly upon maturation, and will germinate with the first adequate rainfall, since they apparently have no dormancy. Plants have an extensive root system, which can reach layers of permanent moisture (Marshall, Parson, and Hutchinson, 1937). These characteristics seem to account for the primary hilltop distribution. The capacity of this species for wind dissemination may also account for its greater range, as compared to the other species in subg. *Articulata. Gossypium australe* F. Muell., native to arid areas of Australia, may have been disseminated in a similar manner (Fryxell, 1965).

SOUTH AFRICA: NATAL: Zululand: Ntambanana, *Taylor s.n.* (PRE); 9 mi from Hluhluwe, Reserve gate, Hlabisa rd, *Wells 2048* (PRE); Umfolosi Game Reserve, 600 ft alt, *Ward 3240* (PRE), *Edwards 3298* (PRE); Ingwauuma, red sand nr vley, *Strey 4757* (PRE). TRANSVAAL: Barberton Distr.: Komati Poort, alt 1000 ft, *Schlechter 11770* (BM, BR, G, L, LE, MO, P, S, US, Z), *Rogers 12624* (Z), *22389* (Z); Lebombo Flats, *Strey 4028* (PRE); Kruger National Park, Nelspruit, 5½ mi N of Malelane, 1000 ft, *Codd 5229* (PRE); Skukuza, on brackish land, 1000 ft alt, *v. d. Schijff 3409* (MO), 3938 (PRE).

SWAZILAND: Stegi to eastern foot of Lubombo, *Burtt-Davy 10572* (PRE); Bremersdorp, *Wood s.n.,* 25 Apr 1927 (PRE); Sipofaneni, *Murdoch 123* (TAES).

MOZAMBIQUE: SUL DO SAVE: Sabie, Moambo, *Pedrogão 27* (LIL), *225* (LIL); Moamba, *Harland s.n.,* 1930 (C); Umbeluzi, *Borle 257* (BM), *551* (PRE), *Lemos 127* (LIL). Marracuene, *Pedro & Pedrogão 643A* (LIL-p.p.), *663* (LIL); *de Carvalho 219* (BM);

Fig. 7. Distribution of *C. gerrardii* ● and *C. heteroclada* ○. Fig. 8. Distribution of *C. hildebrandtii* ●, *C. chiarugii* ⊙, *C. somaliana* ×, *C. welshii* ○, and *C. hearnii* ▲.

Boane, *Braga* 82 (Z); Guijá, *Pedro & Pedrogão 2114* (LIL); Goba, *Wood* 6828 (PRE); bei Pisini zwischen Lebombo und Delgao Bai, *Schenck* 825 (Z); *Myre & Balsinhas* 1663 (BM).

TANZANIA: LUSHOTO DISTR.: 3 mi NW of Mombo, on waterlogged soil, alluvial plain, 425 m, *Drummond & Hemsley* 2285 (B, BR, FI).

IN CULTIVATION: *Fryxell 14001* (ARIZ, TAES); *Fryxell 14007* (provenance: Sipofaneni, Swaziland) (TAES).

3. *Cienfuegosia welshii* (T. Anders.) Garcke, Eichl. Bot. Jahrb. Bot. Gard. Berl. **2:** 337, 1883 (as *C. Welshii*).

Hibiscus Welshii T. Anders., Jour. Linn. Soc., London **5** (Suppl. 1): 8, 1860 [Type: Aden, rarissime: *Hook, f.* & *T.* (K-n.v.)].
Fugosia Welschii Hochr., Ann. Cons. & Jard. Bot., Genève **4**: 174, 1900.

Illustrations: Fig. 18, d-g; also Anderson (loc. cit.) t. 1; Janda (1937) Figs. 27, 33; Fryxell (1968) Fig. 3,c.

Upright subshrub from woody rootstock. Stems woody, glabrous, punctate. Leaves 5-ranked; 5-veined, reniform, slightly 3-lobed, denticulate, glabrous (sometimes sparingly scabrous on veins), about twice as broad as long, punctate; punctae often more prevalent on veins (below) and as marginal row. Foliar nectaries 3, medially to sub-apically positioned. Petioles as long as or longer than lamina, canaliculate, scabrous especially on upper side (hairs ½-1 mm) or sometimes glabrate in age. Stipules inconspicuous (1-4 mm), subulate, scabrous. Peduncles 1- (rarely 2-) flowered, articulate and with small bract near center, glabrous,

punctate, often exceeding leaves (1-7 cm), nectaries large. Involucel bractlets 1-2 mm, glabrous, punctate, central bractlet of each group often exceeding lateral bractlets. Calyx ½-1 cm, minutely pilose to glabrate, costulate, prominently punctate (punctae ⅓ mm, distributed in rows along veins throughout calyx); lobes shallow, 3-ribbed, apically pubescent within. Petals 2-3 cm, pale yellow or cream-colored with dark-maroon basal spot covering ⅓ of petal, sparingly punctate. Androecium epunctate, dark maroon, anther mass globose; pollen yellowish. Style epunctate, exceeding androecium; stigma dark purple, pubescent. Fruit 3-4-loculed, prominently punctate (punctae ⅓ mm diam.), minutely and sparsely pilose without, glabrous within, elongate (7-10 mm broad, 12-30 mm long). Seeds 4-5 mm, copiously hairy; hairs fulvous, loosely appressed to nearly straight, to 8 mm. Embryo epunctate, but with pinkish punctae developing on mesocotyl and translucent punctae developing as a single marginal row on the cotyledons upon germination. Chromosome number: $n = 11$.

The vernacular name *"Blambal"* is recorded on Gooding's specimen from Somalia, and Hearn (1968) notes that in southern Yemen the term *"atab baladi"* (cotton of the country) is applied to *Cienfuegosia* spp. as well as *Gossypium* spp.

Distribution (Fig. 8): This species occurs under very arid circumstances in Aden, as well as in Somalia below 700 m. Brettell (1966) states that *C. welshii* "is to be found in some profusion" in the Jebel Sirah range of mountains just to the east of Dirgag. Hearn (1968) cites additional locations and indicates its altitudinal range to be up to several hundred meters above sea level. Hutchinson (1947) noted a greater range of variability, at least in leaf form, in material from Somalia, which he retained in *C. welshii*. Examination of the specimens, however, indicates that specific differences exist in this material that merit taxonomic recognition (Fryxell, 1967a). The separation of the following species *(C. somaliana)* provides this distinction.

SOUTHERN YEMEN (ADEN): Ad fances montis Scham-Scham: *Deflers s.n.*, 3 Apr 1886 (Z), *Deflers 60* (K, P); Goldmore Valley, *Schweinfurth 75* (BM, C, Z); 2 m alt, *Hildebrandt 780a* (BM, LE); *Beccari s.n.*, Mar 1870 (FI); *Waring 19* (K).

SOMALIA: Los Anod, 2300 ft alt, *Hemming 2187* (K); Mordale, alt 740 m, *Gooding 207* (4) (K).

IN CULTIVATION: *Fryxell 14006* (TAES).

4. *Cienfuegosia somaliana* Fryx., Britt. **19:** 33, 1967. [Type: Gan Libah, Urgo/Jilbadaig, 11 July 1945, *Glover & Gilliland 1206*, (Holotype: K)].

Illustrations: Fig. 18, a-c; also Fryxell (1967a) Fig. 1,g, (1968) Fig. 3,d.

Subshrub with odoriferous foliage. Stems angled, punctate, minutely puberulent (hairs ca. 0.1 mm, often simple) becoming glabrate. Leaves 3-ranked; 3-5-veined, 8-25 mm long, somewhat broader, 3-lobed to deeply dissected, having characteristic musky odor when handled; leaf segments obovate to linear, secondarily divided, dentate, punctate (especially on margins), margins minutely ciliate, otherwise puberulent to glabrate; foliar nectaries 1-3 (or rarely lacking), medial, inconspicuous. Petiole minutely puberulent (most densely so near juncture with lamina) to glabrate, about equaling lamina. Stipules minute (2-6 mm), triangular, puberulent to glabrate, caducous. Peduncles ½-2½ cm, minutely

puberulent to glabrate, punctate, articulate and bracteate near base. Involucel of ca 9 unequal bractlets, imperfectly arranged in 3 groups; bractlets triangular, 2-5 mm, punctate, puberulent to glabrate, central one of each group often longest. Calyx 8-10 mm, costulate, punctate (punctae translucent); lobes shallow, 3-ribbed (intercostal areas scarious), minutely puberulent to glabrate without, sparingly short-pubescent at apices within. Petals 15-25 mm, prominently punctate (punctae dark red), bright yellow with large maroon spot covering basal half. Androecium maroon; anther masses globose; pollen yellow. Styles slender, exceeding androecium and nearly equaling petals, red, epunctate; stigmas decurrent, maroon, glabrous. Fruit ascending-pilose when young, becoming minutely and sparsely pilose at maturity, prominently punctate (punctae ⅓ mm diam.), 3-loculed, about twice as long as broad. Seeds 5-7 mm, copiously hairy, the hairs nearly straight, tan or brown, 6-8 mm. Embryo light-punctate along cotyledonary margin, punctae darken upon germination, those of the mesocotyl becoming bright red. Chromosome number: $n = 11$.

Distribution (Fig. 8): Somalia: in mountains along northern coast; Ethiopia: in vicinity of Dire Dawa. *Cienfuegosia somaliana* occurs at elevations from 900 m to 1700 m, while *C. welshii* occurs from sea level up to 700 m.

The vernacular name *"biei"* is recorded on *Bally 9674*.

As previously noted (p. 189), these plants were included in *C. welshii* by Hutchinson (1947) who referred to a range of variability in leaf form. However, the two taxa that are here distinguished are differentiated by more than variation in leaf form, as is shown in the following tabulation (modified from Fryxell, 1967a, Table 1).

	C. welshii	*C. somaliana*
Foliage:	Non-odoriferous	Odoriferous
Leaf form:	Broader than long, reniform, denticulate	Slightly broader than long, suborbicular to dissected, dentate
Vestiture:	Scabrous (on stipules, petioles, and underside of leaf)	Minutely puberulent to glabrate
Petiole length:	Greater than lamina	Equaling lamina
Peduncle length:	3-7 cm, medially articulate	½-2½ cm, basally articulate
Petal color:	Pale yellow with small spot covering lower third of petal, sparingly punctate	Bright yellow with large spot covering lower half of petal, prominently punctate
Stigmas:	Pubescent	Glabrous
Seed length:	4-5 mm	5-7 mm

SOMALIA: GAN LIBAH: Urgo/Jilbadaig, *Glover & Gilliland 1206* (K), Golis Range, *Glover & Gilliland 1216* (K); on first terrace facing N, 5100 ft, aromatic leaves, *Bally 11910* (K). HARGEISA: sandy ground by stream bed, aromatic, 4300 ft, *Gillett 4239* (FI, K, P); Fodjor Esc. W of Shiek; 5000 ft, rocky hill slope, lemon scented, *Bally 9674* (K); Sirad'ad, Yamhada: nr rd from Erigavo to Mait, W of 19 on Tabah Rd, alt 5500 ft, dry soil on crest of spur, leaves fragrant when crushed, *Newbould 716* (K).

ETHIOPIA: Generally dry area, 2 km SE of Dire Dawa, 3000 ft alt, *Getahun s.n.*, 11 Nov 1965 (TAES).

IN CULTIVATION: *Fryxell s.n.* (provenance: Dire Dawa, Ethiopia) (BM, CTES, TAES).

5. *Cienfuegosia chiarugii* Chiov., Fl. Som. 101, 1929 [Type: Somalia, Costa dei Migiurtini: Altipiano calcareo presso Hafùn, 23 May 1924, *Puccioni & Stefanini 617 (680)* (Holotype: FI)].

Illustrations: Chiovenda (1929) Pl. III, fig. 3 (not Pl. III, fig. 1 as stated by Chiovenda, nor Pl. I, fig. 3 as cited in Index Londonensis.)

Low woody subshrub. Stems glabrous, punctate. Leaves cuneiform-obovate, entire, obtuse to weakly and irregularly undulate apically, glabrous, punctate, almost as broad as long; foliar nectary lacking. Petioles 3-4 mm (ca ⅙ length of lamina), slightly scabrous near juncture with lamina. Stipules minute (1 mm), subulate. Peduncles 3-4 mm, prominently punctate, glabrate, basally articulate with small scale at articulation (articulation obscured by shortness of structures). Involucel bractlets 1-1½ mm, prominently punctate, glabrate. Calyx 1 cm, ecostulate, prominently punctate (punctae denser toward apices of lobes), becoming torn and pseudo-bilabiate in flower, glabrate without, pilose within (on apices of lobes); lobes short. Petals 1½ cm, punctate.

In addition Chiovenda's description adds: Androecium purple; filaments 6 mm. Style simple; stigma clavate, 3-lobed. Petals violet. The fruits and seeds are unknown.

Chiovenda's complete and generally accurate diagnosis of this species included the description of a gamophyllous involucel and, indeed, emphasized it as a distinctive feature. Moreover, he used this trait as the sole diagnostic feature for sect. *Synodontos,* which he erected to include this species (cf. p. 196). Examination of the type indicates that the involucel is not gamophyllous but is similar to that typical of the genus with bractlets wholly distinct. Chiovenda's description must therefore be amended.

Distribution (Fig. 8): Known only from the type locality, in northeastern Somalia, the only region of Africa beyond 50° east longitude.

SOMALIA: Costa dei Migiurtini: Altipiano calcareo presso Hafùn, *Puccioni & Stefanini 617 (680)* (FI).

6. *Cienfuegosia hearnii* Fryx., Britt. **19:** 33, 1967 [Type: In cultivation, Tempe, Arizona, *Fryxell 14005* (Holotype: ARIZ, isotypes: LE, SD, TAES, US)].

Illustrations: Fig. 18, h-k; also Fryxell (1967a) Fig. 1, e-f, (1968) Fig. 3,e.

Low perennial subshrub, branches erect, foliage odoriferous. Stems glabrate. Leaves 5-ranked, leathery, rhomboid to subreniform, sometimes weakly 3-lobed, coarsely serrate, undulate to crisped, cuneate to truncate, glabrous, 3-5 nerved, 15-20 mm long, 20-25 mm broad (or smaller under stressed conditions), with characteristic musky odor when handled; foliar nectaries 1-3, median. Petioles 5-15 mm long, scabrous near juncture with lamina, sparingly so elsewhere. Stipules minute (1 mm), sessile, subulate, glabrous, caducous. Peduncle axillary, 5-20 mm, articulate near center or below with small bract at articulation, punctate, glabrous, nectaries large. Involucel bractlets triangular, 2 mm long, punctate. Calyx 7-8 mm, costulate, scarious in intercostal areas, densely to sparingly punctate (sometimes epunctate); lobes shallow, ovate, 3-5-ribbed. Petals 2 cm,

sparingly punctate, dark purple to roseate (rarely pallid) within, greenish margin without (where exposed in bud), very dark spot covering lower third of petal within. Anther mass ellipsoid; staminal column dark purple, punctate; anthers numerous, dark purple; pollen cream-colored to orange. Style yellowish, punctate, exceeding androecium; stigma dark purple, pubescent. Fruit globose or slightly elongated, 1-1½ cm long, 3-4 loculed, rostrate, weakly strigose, punctate. Seeds 5-6 mm long, densely sericeous; hairs creamy-tan, very loosely appressed (nearly straight), up to 8 mm long. Embryo epunctate, but with red punctae developing on mesocotyl and translucent punctae as single marginal row on cotyledons upon germination. Chromosome number: $n = 11$.

The original description of this species, which was based on cultivated material from a single accession, may now be broadened to account for the variation found in a wider range of material. Although the collections cited exhibit an appreciable variability in several traits, they appear to represent but a single taxon.

Four vernacular names are on record for *C. hearnii*. Hearn (1968) refers to the name *"atab baladi"* ("cotton of the country") used for both *Cienfuegosia* spp. and *Gossypium* spp. in Southern Yemen. In addition, collectors' notes record *"Lawa" (Thesiger s.n.), "Tamrat el Ghanam"* ("sheep browse"), and *"Shejra el Ham"* ("plant of distress"), the latter two from *Maxwell-Darling 94*.

Distribution (Fig. 8): Hearn (1968) states that this species is known from three localities on the southern margin of the Arabian peninsula growing in the coastal littoral and to an altitude of 1000 m. Additional specimens *(Thesiger s.n.* & *Popov et al. 4236)* extend this distribution more than 100 miles inland. This is apparently an environment of extreme aridity.

SOUTHERN ARABIA: HADHRAMAUT: Meifa Hajar, on pebbly plain, alt 50 ft, *Maxwell-Darling 94* (BM), *Guichard 122* (BM); Riyan, *Guichard 122A* (BM); Radum, alt 100 ft, *Hearn 4* (BM); Wad Mahfad, 2000 ft, in gypseous silt of wadi bed, *Popov et al. 4277* (BM); edge of northern Jol nr Zamuk, 3000 ft, gravelly wadi bed, *Popov et al. 4236* (BM); Halaya Well, *Thesiger s.n.*, 16 Feb 1946 (BM).
IN CULTIVATION: Tempe, Arizona, *P. Fryxell 14005* (ARIZ, LE, SD, TAES, US).

3. SECT. **Dioica** Fryxell, sect. nov.

Folia cuneata, simplicia vel exigua lobata. Flores dimorphi, in racemis brevibus antequam folia portata sunt. Foliola involucrorum tria.

Plant glabrous. Stems angular, punctate. Leaves simple to weakly lobed, cuneate, entire, with medial to subapical foliar nectaries. Petioles short. Stipules linear, minute. Flowers arising in short racemes from ground level before leaves. Peduncles elongate. Involucral nectaries lacking. Involucel irregular, typically of 3 bracts; each triangular, punctate. Calyx costulate, punctate (punctae prominent, sparse); lobes ovate, apiculate, 3-5-ribbed. Flowers dimorphic. Petals pink, nearly epunctate. Androecium pallid, narrow. Fruit obovoid, glabrous, punctate. Seeds densely comose; hairs straight, rufous-red.
Type species: *Cienfuegosia heteroclada* Sprague. The name of sect. *Dioica* is chosen in reference to the dioecious condition found in its only species.

7. *Cienfuegosia heteroclada* Sprague, Kew Bull. **1907:** 48, 1907 [Type: Northern Nigeria, Kontagora, in the bush after burning, *Dalziel 122*. (Holotype: K-n.v., isotype: G)].

Fugosia heteroclada Sprague, op. cit., 49, pro syn.

Illustrations: Fig. 17, f-g; also Hutchinson & Dalziel (1928) Fig. 112.

Much-reduced subshrub from woody rootstock. Species dioecious. Stems ridged; inflorescence a short raceme, exceeded by vegetative stems. Leaves elliptic to obovate, or sometimes apically 2-3-lobed or 2-5-dentate, glabrous above and below, 3-5-nerved. Foliar nectaries 1-3, the central one near apex of leaf, the laterals near middle. Petioles canaliculate, glabrous, punctate. Stipules 2-5 mm, glabrous. Rachis of inflorescence punctate, glabrous, angular, pallid, pedicels arising from nodes of rachis, bracteate at nodes, 1-3 cm, glabrous. Involucral bracts irregular in form and number; typically 3, each triangular (or sometimes apically laciniate or 2-3-parted, suggesting a fusion of parts), 4-5 mm long, 2 mm broad, glabrous. Calyx infundibular to campanulate, 9-15 mm, glabrous, punctae sometimes confined to tips of lobes, green, sometimes torn in flower; lobes sometimes suffused with purple. Petals 2-3 cm. Androecium 6-12 mm, pallid; filaments 1-3 mm. (Pistillate flowers not seen.) Fruit 18 mm long, ca. 1 cm broad. Seeds ca. 8 mm, hairs ca. 1 cm long.

Emsley (1957) notes the existence of floral dimorphism in this species and states that about 90% of the plants are staminate, 10% pistillate. The illustration presented by Hutchinson and Dalziel (1928) shows a flower with a greatly reduced gynoecium that apparently represents the staminate form. The occurrence of dioecism is unknown elsewhere in *Cienfuegosia*, and occurs elsewhere in the tribe *Gossypieae* only in the genus *Hampea*.

Distribution (Fig. 7): Nigeria: vicinity of Kontagora (and Naraguta?); Ghana. It has a limited distribution, although described as "locally abundant" (Emsley, 1957). Plants of *C. heteroclada* are nearly acaulescent, flower directly from the perennial rootstock, and fruit in a relatively short time. The species is thus well-adapted to the periodically burned-over savannahs in which it occurs.

NIGERIA: Kontagora, Northern Nigeria, *Dalziel 122* (G).

GHANA: Tongo Hills, E side of Zuarungu, *Morton A 1286* (K); Tumu, nr Rest House, *Ahiekpor s.n.*, 10 June 1966 (GC) *Adams & Akpabla 4364* (GC); roadside ca 2 mi S of Han, *Adams 4013* (GC); footpath from Pwalgu Bridge to Gbeigo village, *Enti & Agyakwa s.n.*, 20 Jan 1966 (GC).

II SUBG. CIENFUEGOSIA

Cienfuegosia Cav., Diss. **3:** 174, 1787 (as genus).

Leaves of variable form, generally punctate, but often obscurely so; foliar nectaries lacking. Flowers axillary, solitary, on unjointed peduncles (or peduncles sometimes articulated in *C. affinis*). Involucral nectaries 3 or none. Involucel of 8-12 bractlets (or involucel lacking in section *Friesia*); bractlets ungrouped, minute and subulate to prominent and lanceolate or spatulate. Calyx punctate (punctae sometimes obscure); lobes acute to acuminate. Petals punctate or epunctate, yellow (or nearly white in *C. tripartita*) with dark spot on claw often having yellow radii, or without spot. Stigmas decurrent or capitate, 3-5-lobed; styles

sometimes divided apically. Fruits glabrous or densely villous, punctate or epunctate, sometimes with hairs on inner suture line (in sect. *Cienfuegosia*).
Type species: The type of subg. *Cienfuegosia* is the type of the genus *Cienfuegosia*, *C. digitata* Cav.

KEY TO SECTIONS OF SUBGENUS CIENFUEGOSIA

a. Stigmas decurrent (or at most subcapitate); fruits glabrous, epunctate; bractlets of involucel ca. 9, usually minute, linear-subulate; inner suture hairs present on capsule; involucral nectaries usually present ..... 4. *Cienfuegosia* (p. 205)
aa. Stigmas capitate; fruits glabrous or pubescent, usually punctate; bractlets of involucel 8-10, lanceolate to spatulate, subequal to calyx, or lacking; suture hairs lacking; involucral nectaries lacking:
  b. Upright shrub or perennial herb; stipules filiform; involucel subequal to calyx; petals punctate ..... 5. *Robusta* (p. 216)
  bb. Perennial herb, decumbent or ascending; stipules subulate or auriculate; involucel subequal to calyx or lacking; petals epunctate (or at most obscurely punctate).
    c. Involucel subequal to calyx: stipules subulate, symmetrical; plants procumbent or ascending ..... 6. *Paraguayana* (p. 220)
    cc. Involucel lacking; stipules auriculate, asymmetrical; plants procumbent ..... 7. *Friesia* (p. 228)

4. SECT. CIENFUEGOSIA

Cienfuegosia Cav., Diss. 3: 174, 1787 (as genus).

Herbs or subshrubs arising from perennial woody rootstock. Stems ascending, green, 5-angled, minutely scurfy-puberulent to glabrous, obscurely punctate. Leaves entire, tripartite, or digitately divided, minutely puberulent to glabrous, punctate (but punctae obscure and usually visible only with magnification and careful illumination). Petioles canaliculate, minutely punctate, glabrous or minutely puberulent especially near juncture with lamina. Stipules minute. Peduncles glabrous to scurfy-puberulent, incrassate above, minutely punctate, surmounted by 3 involucral nectaries (sometimes lacking). Involucel of ca. 9 elements; bractlets distinct, minute, filiform, persistent. Calyx 15-veined, prominently punctate, puberulent to glabrate; lobes acuminate or sometimes acute. Petals epunctate, yellow (sometimes white) with or without dark spot on claw. Stigmas decurrent (or subcapitate in *C. subternata*), 3-lobed; styles undivided. Fruits epunctate, 3-valved, glabrous without, with hairs on inner suture line.

Lewton (1925) drew attention to the capsulary fringe of hairs that characterizes this section, as it is found in *C. heterophylla* (Vent.) Garcke and *C. yucatanensis* Millsp.

One of the most striking features of this section is the variability of leaf form within plants of all of the species. When speaking of leaf form in this group, therefore, it is necessary to use the concept of "leaf spectrum" (Melville, 1953).
Type species: The type of sect. *Cienfuegosia* is the type of subg. *Cienfuegosia*, *C. digitata* Cav.

KEY TO SPECIES OF SECTION CIENFUEGOSIA

a. Leaves deeply digitately divided, often secondarily so; anthers 5-ranked; petal spot (when present) and staminal column carmine; distribution African ..... 8. *C. digitata*
aa. Leaves entire, lobed, rarely with secondary divisions as above or trifoliolate; anthers usually unranked; petal spot and staminal column dark-maroon (or spot

absent and staminal column light); distribution American.
b. Leaves narrowly lanceolate to oblong, entire (lower leaves rarely trilobed); petiole glabrous; involucral nectaries usually lacking; corolla rotate; petals yellow, small (1-2 cm), lacking basal spot; pollen yellow; distribution Yucatan, Florida, Bahamas, Cuba . . . . . 9. *C. yucatanensis*
bb. Leaves broad and entire or variously divided; petiole puberulent at distal end; involucral nectaries present; corolla campanulate; petals yellow or white with basal spot; pollen orange or reddish; distribution Middle or South American.
c. Leaves broadly ovate to moderately 3-lobed; distribution northern South America and Middle America.
d. Style and stigma exceeding androecium; involucral bractlets 3-10 mm; leaves apiculate . . . . . 10. *C. rosei*
dd. Style and stigma largely included within androecium; involucral bractlets 1-3 mm; leaves usually acute to obtuse . . . . . 11. *C. heterophylla*
cc. Leaves large, entire to deeply divided or tripartite.
e. Leaves trifoliolate; leaflets narrow; petals yellow, with large basal spot having yellow radii; distribution Paraguay . . . . . 12. *C. subternata*
ee. Leaves entire, cuneiform to variously divided (sometimes secondarily so); petals white or pale yellow, with small basal spot usually lacking radii; distribution Peru and Ecuador . . . 13. *C. tripartita*

8. *Cienfuegosia digitata* Cav., Diss. **3:** 174, 1787 [Type: Senegal: *Adanson 145A* (Holotype: P, isotypes: MA, P)].

Fugosia digitata Pers., Syn. **2:** 240, 1806.
Hibiscus Cavanillesii Kuntze, Rev. Gen. Pl. **1:** 69, 1891 (based on *Cienfugosia digitata* Cav.) non *H. cavanillesianus* H.B.K.
C. digitata var. *lineariloba* Hochr., Ann. Cons. Jard. Bot., Genève **6:** 56, 1902 [Type: S.W. Africa: Grootfontein, Hereroland, 21 May 1899, *Dinter* 669 (Z)].
C. junciformis A. Chev., Rev. Bot. Appliq. **30:** 267, 1950 [Type: Niger: *Chevalier s.n.* 16 Feb 1950 (PAT ? -n.v.)].
C. junciformis var. *ruyssenii* A. Chev., loc. cit. 268, (as *ruysseni*) [Type: Niger: *Ruyssen s.n.* (PAT ? -n.v.)].

Illustrations: Fig. 20, a-d; also Cavanilles (1787) Pl. 72, fig. 2, f-m; Lamarck (1819) iii, t. 577 (n.v.); Chevalier (loc. cit.) Pl. XII; Fryxell (1968) Fig. 3,h.

Plant minutely puberulent on meristems, becoming essentially glabrate throughout. Stems minutely and obscurely punctate. Leaves 5-ranked, digitately 3-5-parted; lobes often secondarily divided apically, sometimes simple, lanceolate to oblanceolate, acute. Petioles punctate, ca. ½ length of lamina or less, minutely puberulent near juncture with lamina. Stipules 1-3 mm, linear, pubescent (sometimes glabrate). Peduncles axillary, solitary, unjointed, costulate, obscurely punctate, minutely puberulent to glabrate, 1-4 cm long (½-1½ times length of leaf), usually surmounted by 3 prominent involucral nectaries. Involucel bractlets 1-4 mm, usually glabrate. Calyx 1-1½ cm long, minutely puberulent to glabrate, costulate (intercostal areas whitish), punctae ¼ mm diam., deeply lobed; lobes 3-ribbed, acuminate (sometimes acute). Petals yellow with carmine spot having yellow radii on claw (spot rarely lacking), 1½-2½ cm (rarely larger), with undulate margin. Androecium carmine or pale; anther mass globose to obovate; anthers numerous, arranged in 5 ranks opposite the petals (or ranks divided to appear as 10); pollen orange. Style pallid, exceeding androecium; stigma decurrent, pubescent, whitish. Fruit ovoid, 8-12 mm, copiously hairy (hairs 2 mm) on internal suture margins. Seeds 3-4 mm, densely comose; hairs appressed, tan, 6-8 mm long. Embryo epunctate. Chromosome number: $n = 10$.

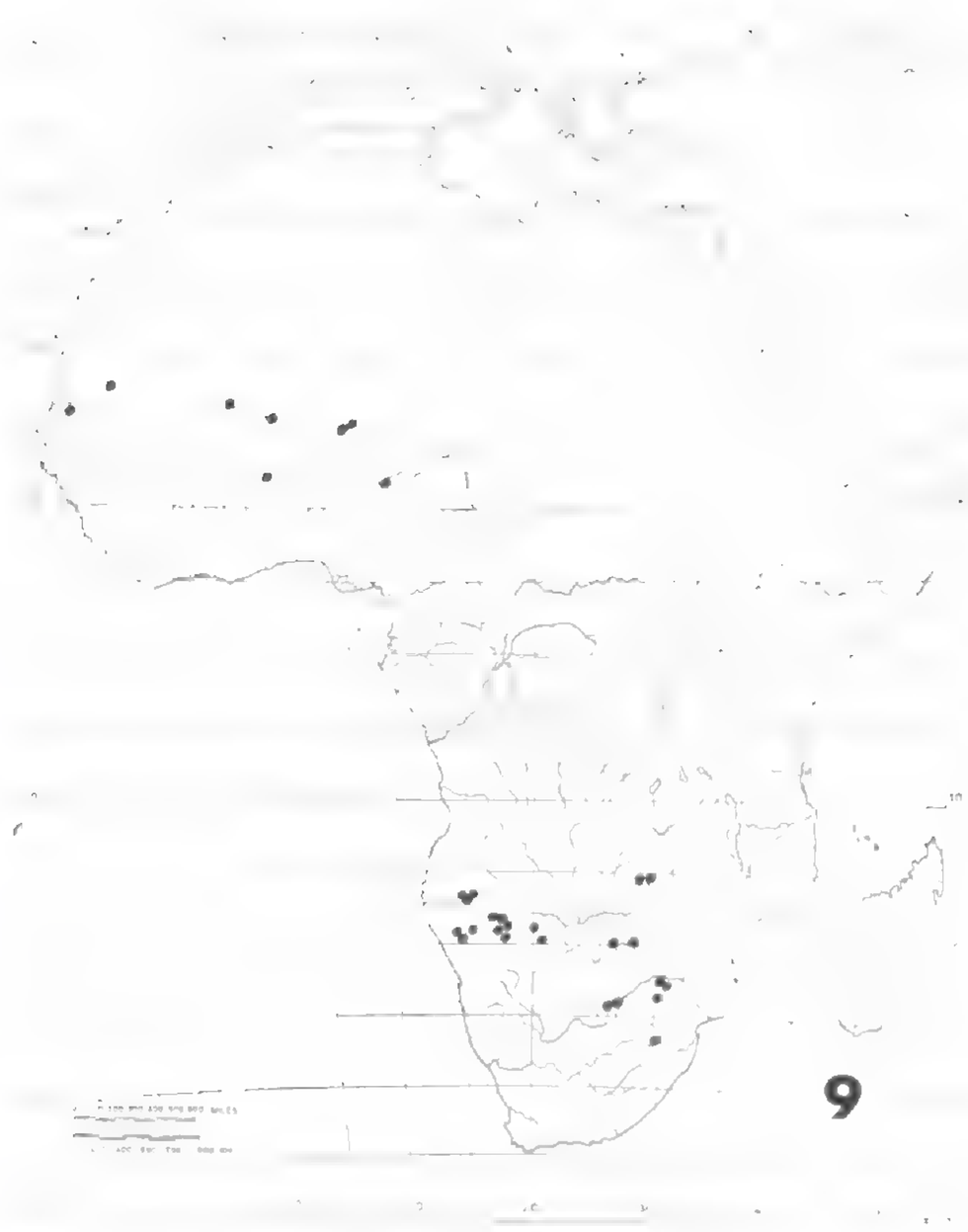


Fig. 9. Distribution of *C. digitata.* Fig. 10. Distribution of *C. yucatanensis.* Fig. 11. Distribution of *C. heterophylla* ▲, *C. affinis* ●, and *C. cuyabensis* ○.

Cienfuegosia digitata is relatively uniform morphologically, although leaf form exhibits considerable developmental plasticity. Herbarium specimens and cultivated plants both show this plasticity. Such phenotypic variation is well within the response potential of an individual plant, as indeed can be noted on the holotype of the species. Hochreutiner's var. *lineariloba* was based on such variation and has therefore been reduced to synonymy.

One aberrant specimen from the Transvaal *(Schlieben 9248)* produced multiple calyx lobes, a tendency not noted elsewhere. Most of the calyces on this specimen have 6 or 7 lobes rather than 5. This plant is, in all other respects, representative of *C. digitata.* The aberration therefore is considered not to have taxonomic significance. Another exceptional plant is *Davey 224,* which lacks a petal spot.

Distribution (Fig. 9): As previously noted (p. 186 and Fryxell, 1967b), this species has a disjunct distribution, occurring in western Africa and in southern Africa, but without any concomitant morphological differentiation. The northern segment of the distribution of *C. digitata* extends from Senegambia and southern Mauritania through Mali and northern Ghana to extreme western Niger and northern Nigeria. Reported occurrences as far east as the Sudan have not been substantiated and possibly refer to specimens of *Gossypium somalense* (Gürke) Hutch., as noted by Knight (1949). The southern segment of the distribution of *C. digitata* extends from the southern parts of Angola and Zambia and northeastern S.W. Africa through Botswana to western Rhodesia and the Transvaal. Lignier & Bey (1905, p. 225) cite a specimen of *Fugosia digitata* from Madagascar in the Herbier Lenormand (CN), but the specimen has not been seen to verify its identity, and no other records from there are known.

MAURITANIA: Tagant Plateau betw Madjeria & Tidjikdje, silty flood plain, *G. 62* (BM).
SENEGAMBIA: *Perrottet* 32 (G), 66 (BM, G, P, S,); Bords du Senegal (Walo)*Perrottet s.n.*, 1831 (G, L); Plaines de Richard, *Perrottet s.n.*, 21 Sep 1824 (G, LE); *Sieber* 58 (G, LE, M?, MO?, OXF?, S, UC); Daganá, *Leprieur 1* (G, L, P); *Adanson 145-A* (MA, P); *Roger 13* (LE); *Berhaut 1344* (BR, Z); *Heudelot s.n.*, 1835 (LE), *s.n.*, 1839 (FI, OXF).
MALI: Ansongo, *Olufsen 385a* (C), *Hagerup 385a* (BR); Goumal (Dioura): *Davey* 224 (K), 233 (B); Env. de Tombouctou, *Legagneux s.n.*, Jun 1920 (L); Gourma : de Fada à Koupéla, *Chevalier 24535* (BR).
NIGERIA: KANO: *Honold 20* (Z).
ANGOLA: Huila betw Humbe and Ruacaná, Morros de Cualeque, Dongoena, c 1150 m, *Exell & Mendonça 2872* (BM); Ruacaná, R Cunene, c 1000 m, *Exell & Mendonça 2694* (BM), *2789* (MO).
SOUTH-WEST AFRICA: GROOTFONTEIN DISTR.: Tsumeb, *Dinter 7459* (B, M), *Meyer 21* (B); Farm Onguma, Gelbholzdüne, *Walter 429* (M, PRE); Farm Fockshof, *Volk 125* (M); Amboland, *Schinz 212* (Z), *213* (Z), *Rautanen 19* (LE, Z), *Dinter 669* (Z). OUTJO DISTR.: Farm Franken, *Walter 2/187* (M); Otuzemba, *Merxmüller & Geiss 1355* (M, PRE); Farm Kaross, *Merxmüller & Geiss 1549* (BM, M); Farm Hazeldene, Karos Block, *deWinter & Leistner 5110* (M). SIMKUE DISTR.: *Story 6509* (PRE); Klein Namutoni, *Breyer 20592* (PRE); Onknanjumi, *Wulfhorst 21* (Z); Ondonga, *Rautanen 401* (Z); Vleyrand (Kalk) bei Naruchas, *Dinter 7215* (B); Gautscha Pan, E of Karakuwise, *Maguire 2183* (PRE).
ZAMBIA: Mazabuka, 3400 ft, *Bebbington 1693* (K), 3300 ft, *Vet Officer 249* (PRE).
BOTSWANA: Northern Bechuanaland betw Mumpswe and Sigara pans, ca 26 mi NNW of mouth of Nata River, Mopane Woodland, 900 m, *Drummond & Seagrief 5215* (BM); Mochudi, *Harbor 6481* (K); Crocodile River, *Klingberg s.n.*, Sep 1876 (S); nr Derdepoort, 3000 ft, *Codd 8873* (PRE).
SOUTH AFRICA: TRANSVAAL: N of Soutpansberg, betw Vivo and Waterpoort rd to Mopane, *Schlieben 9248* (G, M); Soutpansberg, Liliput, *Strey 3493* (PRE), 5 mi S of Grass Valley, Potgietersrust, *Meeuse 9581* (B, PRE); Klippan, Boshveld, *Rehmann 5223* (Z); Besterspu t im Distrikt Blomfontein, *Welti 17* (Z), *Schlechter 4664* (Z).
IN CULTIVATION: *Fryxell 14008* (provenance: Outjo, SW Africa) (TAES).

9. *Cienfuegosia yucatanensis* Millsp., Publ. Field Mus. Nat. Hist. Bot. Ser. **2:** 74, 1900 [*Type:* Yucatan: arid stony soil about 6 km S of Progreso, 5 Mar 1899, *Millspaugh 1693* (Holotype: F-61693)].

Illustrations: Fig. 20, e-g; also Small (1933) p. 860; Fryxell (1968) Fig. 3,i.

Plant glabrous throughout. Stems minutely and obscurely punctate. Leaves entire, oblong to lanceolate, acute, 4-10 (rarely 20) times as long as broad; lower leaves sometimes broader and trilobed. Petioles punctate, ½ length of lamina or less, glabrous. Stipules 1-2 mm, linear, glabrous. Peduncles axillary, solitary,

unjointed, costulate, obscurely punctate, glabrous, 2-5 cm long (½-1½ times length of leaf); involucral nectaries usually lacking (rarely present, small). Involucel of 6-9 ungrouped bractlets; bractlets ½-2 mm, glabrous. Calyx glabrous, costulate (intercostal areas light green), punctae ⅙ mm diam, 8-12 mm, equaling or exceeding fruit, deeply lobed; lobes 3-ribbed, acuminate. Petals yellow throughout, 1-2 cm, opening flat to form a rotate corolla. Androecium pallid, epunctate; anthers few (10-30), unranked; pollen yellow. Style pallid, sparingly punctate, exceeding androecium; stigma decurrent, pubescent, whitish. Fruit 3-(occasionally 4-) valved, 6-8 mm, ovoid, copiously hairy on internal suture margins. Seeds 2-3 mm, densely comose; hairs appressed, greenish-brown, 4-5 mm long. Embryo epunctate. Chromosome number: $n = 10$.

This species appears to be a specialized derivative of *C. heterophylla* (Vent.) Garcke. Its most notable specializations are in leaf form and in flower structure. The flower is small, opens to a fully rotate form, lacks the dark spot at the center characteristic of related species, and has significantly fewer anthers and produces smaller fruits and seeds. Whether or not these floral differences are related to a specific adaptation to local pollinators, is not known.

Small (1933) distinguished between the material from the "northern West Indies" and that (of *C. heterophylla*) from South America but did not associate the former with *C. yucatanensis* from Yucatan. He gave no nomenclatural recognition to the distinction.

Two accessions of *C. yucatanensis* are available in cultivation, one from Yucatan, the other from Great Inagua, Bahamas. The examination of these living plants shows that the two accessions are clearly conspecific, yet that they are demonstrably different in leaf spectrum and in certain other characteristics. The study of additional accessions of this species from different segments of its distribution may reveal distinctions requiring taxonomic recognition, but if so, at no higher rank than that of forma. For the present, no such distinctions are made.

Distribution (Fig. 10): Yucatan: in vicinity of Progreso and Merida; Florida: Grassy Key, Long Key, Lower Matecumbe Key, Lignum Vitae Key, and Key West; Cuba: Prov. Camaguey: Cayo Romano, Cayo Sabinal, and Cayo Guajaba; Bahamas: Great Inagua Island.

Such a distributional pattern, around the southeastern shores of the Gulf of Mexico, suggests salt-water dispersal of seed.

MEXICO: YUCATAN: Progreso, moist open places, *Steere 3019* (F, MEXU, MICH); arid stony soil ca 6 km S of Progreso, *Millspaugh 1693* (F); km 31 Merida Rd, *Lundell & Lundell 8017* (F, GH, MEXU, MICH, TEX, US); *Lukefahr s.n.*, 26 Jul 1964 (GH, LE, SD, TAES); Chichankanab, *Gaumer 1269* (F); rd betw Sisal and Merida, *Schott* 693 (F).

UNITED STATES: FLORIDA: Lower Matecumbe Key, rocky hammocks, *Small et al. 11599* (GH, MICH, MO, S, US), *Small* 8392 (C, M, S, UC), in dry sandy soil, *Moldenke 619* (ILL, MO, S, US), *Buswell 1387* (ARIZ); Lignum Vitae Key, *Blodgett s.n.* (GH), *Chapman 747* (US), *Garber s.n.*, Aug 1877 (GH, PH, US); Grassy Key, coral soil, *Curtiss* 398 (F, GH, LE, M, MO, PH, US); Long Key, *Simpson 469* (F, GH, S, US); Key West, *Chapman s.n.* (US); S. Florida, *Chapman s.n.* (F, MO).

CUBA: CAMAGUEY: Cayo Guajaba, *Shafer 634* (NY), *686* (F, GH, NY, US); Cayo Romano, Lomo de Loro, *Shafer 2639* (F, GH, NY, US); Cayo Sabinal, in a kind of sweet water meadow, *Ekman 15487* (F, G, GH, MO, NY, S, US).

BAHAMAS: Great Inagua, *Dunbar 146* (GH).

IN CULTIVATION: *Fryxell 15013* (provenance: Yucatan) (ARIZ, TAES); *Fryxell s.n.* (provenance: Great Inagua, Bahamas) (C, CTES, GH, MICH, TAES).

10. *Cienfuegosia* **rosei** Fryxell, sp. nov. [Type: MEXICO: Oaxaca: between San Geronimo and La Venta, alt 200 ft, 13 July 1895, *Nelson* 2779, (Holotype: US, isotype: GH)].

Illustration: Fig. 20, o-p.

Frutex humilis, e radice perenni exoriens, puberula dense et minute in meristematibus (pili stellati, ca. 0.2 mm), plus minusve glabrescens omnino. Caules virides, 5-angulati, ascendentes, punctati minute; internodia brevia. Folia ovata et integra vel trilobata moderate, 3-8 cm longa, apiculata, obscure punctata, circa latiora quam longa vel aliquantum angustiora. Petioli canaliculati, punctati, quam laminae ¼-½ longiores, puberuli minute praesertim prope juncturas laminarum. Stipulae 3-7 mm longae, lineares, punctatae, puberulae. Pedunculi axillares, solitarii, inarticulati, incrassati supra, punctati minute, puberuli minute vel glabrati, 2-8½ cm longi, circa longitudines foliorum subtentiorum aequantes vel parum excedentes, 3 nectariis involucellis terminati. Involucella ca. 9 bracteolis inaggregatis formata; bracteolae involucelliorum distinctae, 3-12 mm longae, filiformes vel subspathulatae, interdum punctatae, puberulae vel glabratae, persistentes. Calyces puberuli vel glabrati, costati leniter, punctati (glandibus ad basem tubi calycis seriatis dispositis), 12-25 mm longi, profunde lobati; lobis calycibus 3-costatis, acutis vel acuminatis. Petala epunctata, 2½-3½ cm longa, flava pallida; unguis saepe macula marronina radios flavos habente. Androecia marronina; antheris numerosis (plus quam 30), imperfecte 5-fariam; pollenibus fusco-incarnatis; cumulis antherarum sphericis vel obovatis. Styli unici, punctati, androecia 6-8 mm excedentes. Stigmata decurrentia, marronina, trilobata, pubescentia, petala fere aequantia ad apicem lata. Fructus 3-loculati, epunctati, 10-13 mm, ovoidei, glabri extus, ciliati sparse in margine suturae. Semina 4-5 mm, dense comosa; pili crispipatentes, brunnei pallide, 5-6 mm longi. Chromosomatum numerus: $n = 10$.

Cienfuegosia rosei is in some respects morphologically similar to *C. heterophylla* but may be distinguished from the latter species by: its longer involucral bractlets (and stipules); its apiculate leaves; its larger flowers with the style notably exceeding the androecium rather than largely included within it; and the less prominently punctate calyx but more prominently punctate foliage. The plant appears also to achieve a smaller stature than *C. heterophylla,* with shorter internodes. As indicated in the discussion on phylogeny (p. 189), *C. rosei* is interpreted as having its closest affinity with *C. tripartita.* Its somewhat closer superficial resemblance to *C. heterophylla* is considered to be an example of convergent evolution. Biosystematic studies will permit verification or qualification of this hypothesis.

Rose recognized this plant as a new species in a manuscript name written on the isotype kept at the Gray Herbarium, but the name was never published. Rose's epithet, "humilis," is not taken up in publishing this species because of the possibility of confusion with the name published by Gürke, *C. phlomidifolia* var. *humilis,* even though Gürke's epithet is illegitimate and of different rank. The name *Cienfuegosia rosei* is chosen instead to honor J. N. Rose.

Distribution: Mexico: Oaxaca: in the lowland coastal plain around Tehuantepec. The plant is described by King (1356) as "abundant [in] flat grazed areas [among] cacti and thorny leguminous shrubs", as I can verify from observation of the same site.

MEXICO: OAXACA: betw San Geronimo and La Venta, *Nelson 2779* (GH, US); 4 km NNE of Tehuantepec, *King 1356* (MICH, TEX), *Fryxell 749* (BH, CTES, F, MEXU, MO, NA, TAES, U); 12 km NNE of Tehuantepec, *King 394* (MICH); cerca Juchitán, *Miranda 8551* (MEXU); 7 mi W of Nilotepec, *Fryxell & Bates 906* (BH, TAES).

11. *Cienfuegosia heterophylla* (Vent.) Garcke, Bonpl. **8**: 150, 1860.

Redutea heterophylla Vent., Hort. Cels, *t. 11*, 1800 [Type: *Ventenat s.n.* (Holotype: G, isotypes: B (photo in GH, MO), FI, MO?, P)].

Fugosia heterophylla Spach, Hist. Veg. Phan. **3**: 397, 1834.

Hibiscus Redoutei Kuntze, Rev. Gen. Pl. **1**: 69, 1891 (based on *Redoutea heterophylla* Vent.).

Fugosia punctata Turcz. Bull. Soc. Nat. Mosc. **31**: 196, 1858 [Type: Brazil: Serra de Jacobina, Bahia, *Blanchet 2702* (Isotypes: BM, G, NY, OXF, P)] (non *Fugosia punctata* Cunn. ex Benth. 1863).

Illustrations: Fig. 20, h-k; also Ventenat (1800) t. 11; Redouté (1827) t. 118 (n.v.); Spach (1846) t. 4218; Martius (1892) Pl. 112, fig. 2; Sampaio (1926) Pl. 1, fig. 2 (illustr. of a single seed of doubtful identity, labelled "Flacourtiaceae-Cienfuegosia heterophylla."); Fryxell (1968) Fig. 3,g.

Plant minutely scurfy-puberulent (appearing lepidote) throughout, or glabrate on older foliage. Stems minutely and obscurely punctate. Leaves 5-ranked, entire, broadly ovate (sometimes rhomboid or obovate, rarely rotund) to moderately 3-lobed, acute to obtuse, rarely acuminate or apiculate, 2-3 times as long as broad (or broader, if lobed), ciliate-margined. Petioles punctate, ¼-½ length of lamina, minutely puberulent especially near juncture with lamina. Stipules 2-5 mm, linear, pubescent. Peduncles axillary, solitary, unjointed, costulate, obscurely punctate, minutely puberulent to glabrate, 2-5 cm (rarely longer), approximately equaling or slightly exceeding (rarely greatly exceeding) length of leaf, surmounted by 3 involucral nectaries. Involucel of 9 ungrouped bractlets; bractlets 1-3 mm, glabrate. Calyx minutely puberulent to glabrate, costulate (intercostal areas light green), punctae ⅙ mm diam., 8-15 mm, deeply 5-lobed; lobes 3-ribbed, acute to acuminate. Petals 1-2½ cm, yellow with maroon spot having yellow radii on claw. Androecium maroon; anther mass globose; anthers numerous (> 30); pollen orange. Style pallid, barely exceeding androecium; stigma decurrent, reddish, pubescent. Fruit ovoid, 8-11 mm, copiously hairy (hairs 2 mm) on internal suture margins. Seeds 4 per locule, 3-4 mm, densely comose; hairs appressed, brown or tan, 6-8 mm long. Embryo epunctate. Chromosome number: $n = 10$.

The Geneva specimen from the Herbier de Ventenat is evidently the holotype since it matches Ventenat's plate (executed by Redouté) quite closely, whereas the Paris and Berlin plants do not match it.

Distribution (Fig. 11): Northern Colombia and Venezuela; certain of the Lesser Antilles (Aruba, Margarita, Trinidad, and St. Thomas); Brazil: provinces of Bahia, Piaui, and Ceara (?). Specimens from Oaxaca, Mexico that were ten-

tatively referred to *C. heterophylla* (Fryxell, 1967a), are here segregated as a distinct species, *C. rosei*.

This taxon occurs primarily around the borders of the Caribbean Sea, but it also occurs in northeastern Brazil in what may constitute a distributional disjunction. The Brazilian material is scanty, but differs from the typical form in being more densely puberulent throughout, and in having broadly acute (rather than acuminate) calyx lobes that are less prominently punctate (punctae ca. 1/10 mm diam.). These differences are too slight to merit recognition at any level higher than that of forma. Should the existence of such a taxon be confirmed by future studies, it would, of course, be best established on Turczaninow's description of *Fugosia punctata*.

COLOMBIA: MAGDALENA: in dry soil, La Paz, alt 200 m, *Haught 4352* (US); Hwy, 7 km S of Riohacha, alt 20 m, *Haught 4473* (F, NY, US); Santa Marta,.alt 150 ft, *Smith 779* (F, G, GH, L, MICH, MO, NY, P, PH, S, UC, US); *Wagener 76* (FI, UC).

VENEZUELA: Maracaybo, *Plée s.n.* (P). SUCRE: Peninsula de Paria, *Steyermark & Agostini 91287* (US); Cumaná, *Moritz 529* (BM). BOLIVAR: along water in ditch betw Río Caroní and Ciudad Bolivar, alt 200 m, *Steyermark 57634* (F, NY), *Moritz 1038* (BM, NY, P, US); Orinoco, *Humboldt & Bonpland s.n.* (P).

ANTILLES: ARUBA ISLAND: *Boldingh 6383* (L, NY, P). MARGARITA ISLAND: El Valle, *Miller & Johnston 66* (F, GH, MO, NY, P, US); Porlamar, *Stephens 1* (GH). TRINIDAD: Chacachacare Island, *Britton 521* (GH, NY, US), *Richardson 899* (IJ, US). ST. THOMAS: Krum Bay, *von Eggers 350* (G, L, LE, M, Z), rocky hillside, Paradise Bay, *Britton & Britton 211* (NY, US), *Hjalmarson s.n.*, 24 Mar 1851 (S), *Rose s.n.*, 1-5 Mar 1913 (NY, US), *Krebs s.n.*, 23 Jan 1898 (C), *Raunkiaer s.n.*, 28 Mar 1906 (C), *Blaumer 9* (G).

BRAZIL: PIAUI: *Gardner 2399* (FI, NY-but labelled "Prov. Ceara", OXF); BAHIA: Serra de Jacobina, *Blanchet 2702* (BM, G, NY, OXF, P).

IN CULTIVATION: Hort Cels (from St. Thomas), *Ventenat s.n.* (B (photo in GH, MO), FI, G, MO?, P); (provenance: Isla Margarita, Venezuela) *Fryxell 15004* (ARIZ, TAES); (provenance: Maracay, Venezuela) *Fryxell 15010* (TAES).

12. *Cienfuegosia subternata* (Hassl.) Fryx., Taxon **16:** 321, 1967.

C. heterophylla (Vent.) Garcke subsp. *subternata* Hassl., Repert. Spec. Nov. **7:** 380, 1909 [Type: Peguahó, Sierra de Amambay, Paraguay, *Hassler 10899* (Lectotype: G, specifically the sheet bearing Hassler's complete collection data; isotypes: G-2 additional sheets)].

Illustrations: Fig. 20, l-n.

Plant minutely puberulent on young foliage, becoming glabrate. Stems very obscurely punctate. Leaves trifoliolate, often unifoliolate above, rarely trilobed below; leaflets usually distinct, entire, lanceolate, acute, 7 cm long or less, ca. 1/10 as broad as long. Petioles ¼ length of lamina or less (rarely longer on lower leaves), minutely puberulent especially near juncture with lamina. Stipules 2-3 mm, linear, puberulent. Peduncles axillary, solitary, unjointed, costulate, obscurely punctate, minutely puberulent to glabrate, 3-5 cm long (approximately equaling the leaf), surmounted by 3 involucral nectaries. Involucel of ca. 9 ungrouped bractlets; bractlets 1-3 mm, puberulent to glabrate. Calyx 1-1½ cm, glabrate, costulate (intercostal areas whitish), punctae < ¼ mm diam, deeply lobed; lobes 3-ribbed, acuminate. Petals 2-3 cm, yellow with large (1 cm) maroon spot on claw having yellow radii. Androecium maroon; anther mass globose; anthers numerous (> 40); pollen yellow (?). Style pallid, punctate, glabrous, greatly exceeding androecium (nearly equaling petals); stigma sub-capitate (i.e.,

intermediate between decurrent and capitate forms), dark-red. Fruit ca. 1 cm, copiously hairy (hairs 2 mm) on internal suture margins. Seeds (immature) ca. 3 mm, angular, brownish-pubescent.

This species is a narrow endemic, clearly allied to the other species of this section, most obviously so in the nature of certain of its fruiting structures: involucel, calyx, and capsule. It is distinctive in its trifoliolate leaves and its large flowers with sub-capitate stigmas.

Distribution (Fig. 12): restricted to the valley of the Río Apa in northern Paraguay.

PARAGUAY: in campo humido argilloso, Peguahó, Sierra de Amambay, *Hassler 10899*, (G); Nördl. Paraguay (22-23° lat.) zwischen Río Apa und Río Aquidabán, Centurion, Niederer Camp, Sumpfrand an grasfreie Stelle, *Fiebrig 4022*, (G-4 sheets (photo of 1 in MO), GH, L, M; there are 2 additional sheets at Genève labelled "*K. Fiebrig 5230*" that may be duplicates of *4022*).

13. *Cienfuegosia tripartita* (H.B.K.) Gürke in Mart., Fl. Bras. **12** (3): 578, 1892.

Redoutea tripartita H.B.K. Nov. Gen. Sp. Pl. **5**: 294, 1821 [Type: Peru: Jaen de Bracamoros: *Humboldt & Bonpland s.n.* (Holotype apparently lost; photographs are at MO and NY); Neotype: Peru: Dept. Cajamarca, Prov. Jaen, near the confluence of the Chinchipe and Marañon, 600-800 m, *Weberbauer 6214*, May 1912 (US, isoneotype: F, GH)].

Fugosia tripartita Steud. Nom. ed. II, **1**: 649, 1840.

Hibiscus tripartita Kuntze, Rev. Gen. Pl. **1**: 69, 1891.

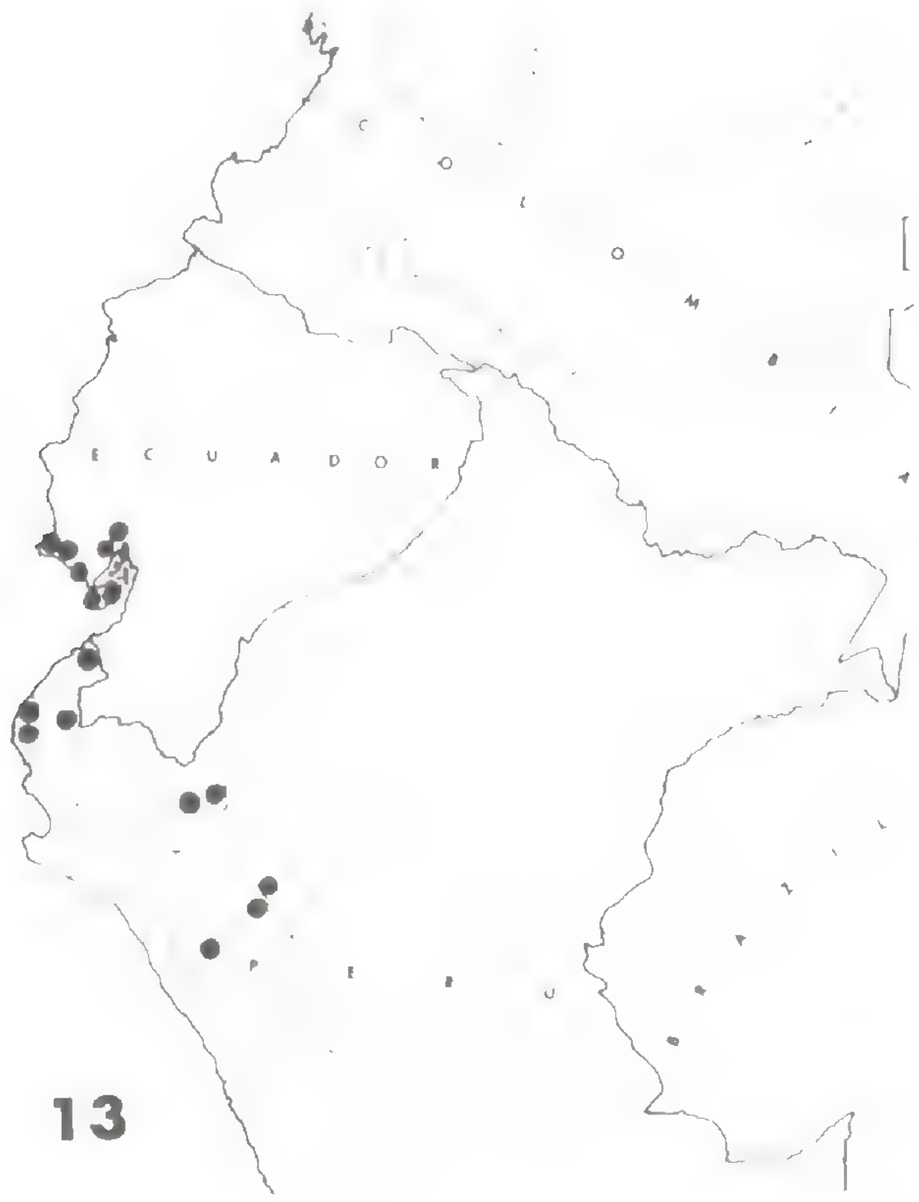
Fugosia cuneata Benth., Bot. Voy. Sulph. 68, 1844 [Type: Ecuador: Guayaquil: *Sinclair s.n.* (K-n.v., US-photo)].

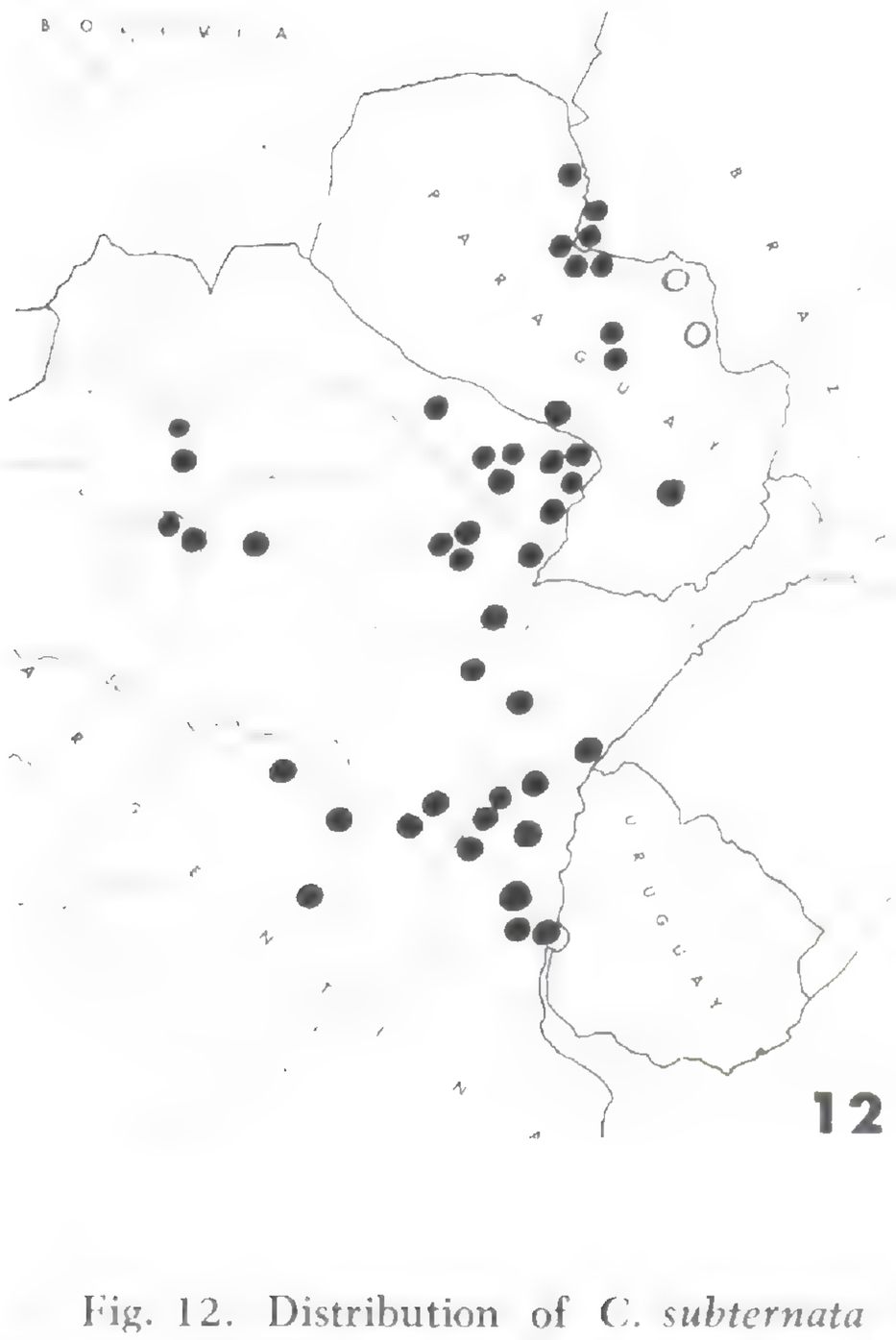
Hibiscus cuneata Kuntze, Rev. Gen. Pl. **1**: 69, 1891.

Cienfuegosia heterophylla var. *cuneata* Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. **13**: 477, 1956.

Illustrations: Fig. 19.

Plant minutely scurfy-puberulent becoming glabrate. Stems punctate, sometimes obscurely so. Leaves of variable form: sometimes ovate-entire or ovate-crenate, more commonly 3- (rarely 5-) lobed in various degrees to completely trifoliolate, 2-7 cm long; leaflets lanceolate to obovate, entire or rarely secondarily divided, sometimes single and narrowly oblong. Petioles usually less than ½ length of lamina, punctate, minutely puberulent near juncture with lamina (rarely puberulent throughout). Stipules linear, 1-3 mm, caducous. Peduncles axillary, solitary, unjointed, costulate, minutely punctate, glabrate, 2-9 cm long (approximately equaling or slightly exceeding length of subtending leaf), usually surmounted by 3 involucral nectaries. Involucel of 9 ungrouped bractlets; bractlets 1-3 mm, rarely longer, glabrous. Calyx glabrate, costulate, prominently punctate (punctae ⅙ mm diam.), 1-1½ cm, deeply lobed; lobes 3-ribbed, acuminate. Petals epunctate (or rarely punctate), pale yellow to white with small maroon spot on claw (usually lacking radii), 3-4 cm (rarely smaller). Androecium maroon (sometimes light); anther mass elliptic; pollen orange. Style pallid, usually greatly exceeding androecium (nearly equaling petals), epunctate, (rarely punctate); stigma decurrent or rarely sub-capitate, pinkish; stigmatic lobes sometimes partially free. Fruit ovoid, 1-1½ cm, copiously hairy (hairs 2 mm) on internal





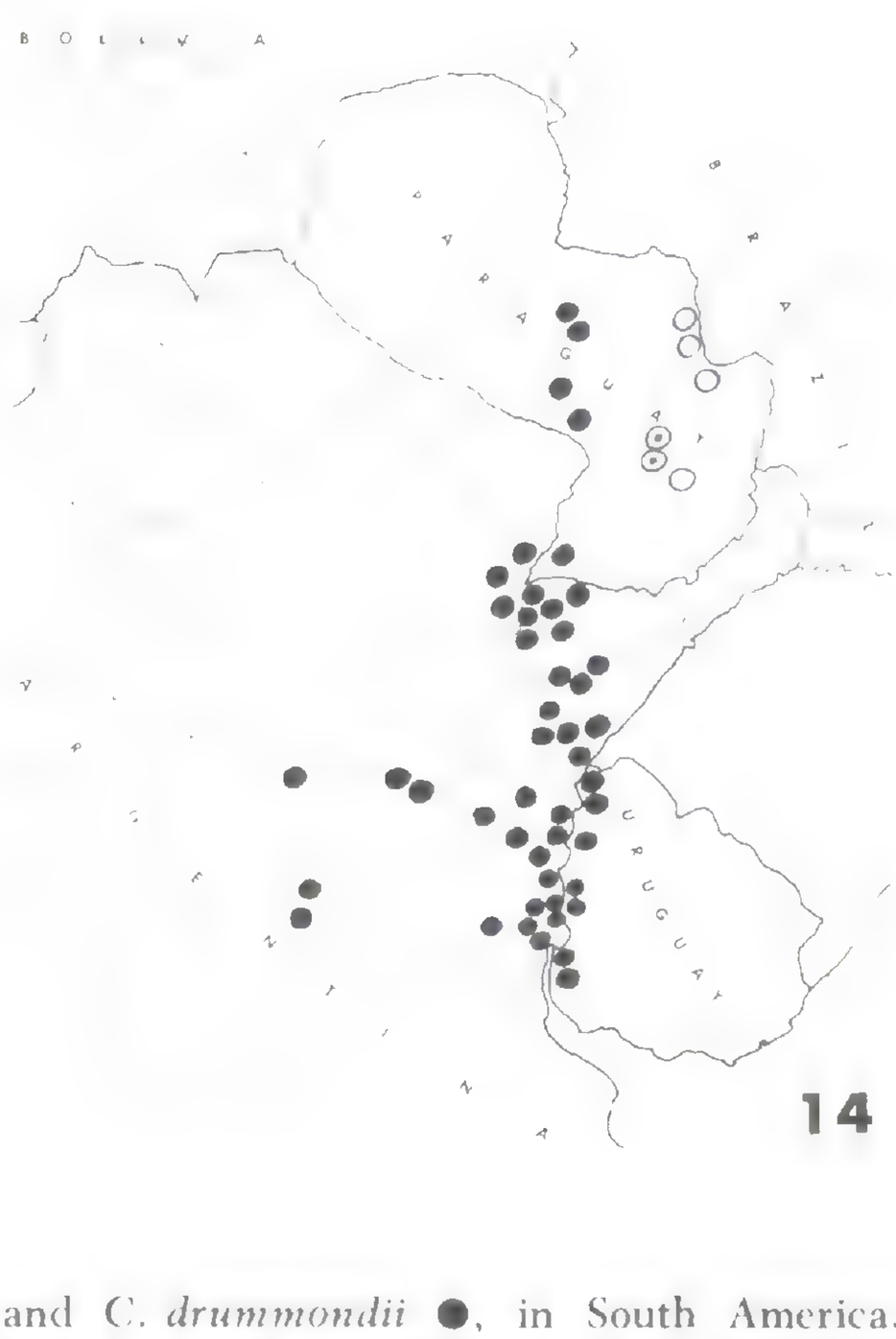


Fig. 12. Distribution of *C. subternata* ○ and *C. drummondii* ●, in South America. Fig. 12a. Distribution of *C. drummondii* in Texas. Fig. 13. Distribution of *C. tripartita*. Fig. 14. Distribution of *C. sulfurea* ●, *C. integrifolia* ○, and *C. subprostrata* ⊙.

suture margins. Seeds 5-9 per locule, 2-3 mm, comose; hairs appressed, tan, ca. 5 mm. Chromosome number: $n = 10$.

The holotype of *Redoutea tripartita* was in the Berlin herbarium and is now apparently lost. Photographs of this plant are in the NY and MO herbaria with the designation W.12836 from the Willdenow collection. The number 3601 also appears on this specimen, although it was not numbered by Humboldt and Bonpland. Apparently there were no isotypes, and no syntypes or paratypes were cited in the original description by Kunth. The situation, therefore, requires the selection of a neotype. One might under the Rules select as neotype either the photograph of the lost holotype or a suitably chosen specimen. Since the holotype was a poor specimen and according to Kunth was wormy, so that he had to rely on Bonpland's notes to some extent in preparing his description, it seems wiser to select a specimen as neotype. The specimen chosen is *Weberbauer 6214* (US-#1496233), which was collected near the type locality and which, in a rather variable species, conforms well to the holotype. Duplicates of this specimen are in F (628149) and GH.

Previous authors (Garcke, 1860; Hassler, Repert. Spec. Nov. **7:** 380, 1909; Svenson, 1946; and Macbride, loc. cit.) noted an alliance between *C. tripartita* and *C. heterophylla,* but only Macbride recognized the alliance nomenclaturally. His choice of Bentham's epithet, *cuneata,* has priority in varietal rank.

The characteristically high degree of variability of leaf form found in sect. *Cienfuegosia* is especially well expressed in *C. tripartita.* The extremes of expression can often be found among the leaves of a single specimen of this species. The extent of this variability is aptly characterized in a collector's note, [*Haught 40* (US)], which says, "Leaves extremely variable in form — if found fossil, how many genera might be founded on those of a single specimen!"

The taxon is also quite variable in certain other respects, which may be best noted in *Hutchison & Wright 5422,* which shows the following atypical characteristics. In this specimen the herbage is more pubescent, the petioles shorter, the black glands more prominent and more widely distributed (even to the petals), and the stigma is of a subcapitate form. These are all deviations in the direction of *C. intermedia.* Further material may reveal a form that deserves taxonomic recognition.

Distribution (Fig. 13): Ecuador: from the Santa Elena peninsula and the vicinity of Guayaquil southward, including the Island of Puna; Peru: provinces of Tumbes and Piura, inland to Cajamarca and Amazonas. This taxon is apparently *not* contiguous with *C. heterophylla* in northern Colombia as has sometimes been implied.

ECUADOR: GUAYAS: Saños, *Asplund 5661* (US); Guayaquil, *Sinclair s.n.* (K-n.v., US-photo). ANCON DISTR.: Santa Elena Peninsula, *Sheppard s.n.* (K); Salinas, nr sea level, *Landeman 46* (K); Chanduy, in litore Maris Pacifici, *Spruce 6393* (BM); Puna, *Eggers 14767* (M), *Andersson 135* (S).

PERU: PIURA: Talara, *Haught 40* (NY, US); near the Amotapes where rain falls nearly every year, *Haught s.n.,* 1928 (F); Cerro Prieto, 20 mi E of Cape Pariñas, 1500 ft alt, *Haught 191* (US). TUMBES: cerca de Zarumilla, alt 30 m, *Ferreyra 5962* (F, US). CAJAMARCA: Prov. Celendin, westl. Talwand des Marañon über Balsas, 2000 m alt, *Weberbauer 4262* (G); Prov. Jaen, nr confluence of Chinchipe and Marañon, 600-800 m,

Weberbauer 6214 (F, GH, US). AMAZONAS: Prov. Chachapoyas, Balsas on Río Marañon and upstream ca 4 km, alt 800 m, *Hutchison & Wright* 5422 (UC, US); *Vidal-Sénège s.n.*, 1876-77 (P).

IN CULTIVATION: (provenance: Playas, Ecuador) *Fryxell s.n.* (BM, TAES); (provenance: Chilete, Peru) *Fryxell s.n.* (TAES).

5. SECT. **Robusta** Fryxell, sect. nov.

Folia elliptica vel trilobata. Stipulae minutae, filiformes. Involucrum 8-10 phyllum; foliolia involucrorum calycem subaequantia. Nectaria involucrorum et foliorum nulla. Stigmata capitata, rubra. Petala punctata. Capsulae glabrae intus.

Plants upright or decumbent, shrubby or herbaceous, densely pubescent to glabrous. Leaves elliptic, acute (occasionally obtuse), or 3-lobed, punctate. Flowers axillary, solitary or rarely multiple, on unjointed peduncles (or peduncles sometimes articulate). Involucral nectaries lacking. Involucel of 8-10 bractlets; bractlets not grouped, prominent, subequal to calyx, distinct, linear-lanceolate to slightly spatulate. Calyx costulate, punctate (punctae sometimes obscured by pubescence), pubescent to glabrous; lobes acute to acuminate. Petals moderate to large, punctate (sometimes obscurely so), yellow with dark spot on claw having yellow radii. Stigmas capitate, red. Style greatly exceeding androecium, undivided. Fruits glabrous or densely villous without, glabrous within.

Type species: The type of sect. *Robusta* is *Cienfuegosia affinis* (H.B.K.) Hochr. The name of the section is chosen in reference to the larger, shrubbier growth habit found in the type species of this section.

KEY TO SPECIES OF SECTION ROBUSTA

a. Leaves ovate to elliptic, entire, short petioled (ca 1/5-1/10 lamina length).
  b. Plants densely pubescent except on upper surface of leaf (rarely glabrate); fruit ascending-villous; seed sub-glabrous to minutely puberulent . . . . . 14. *C. affinis*
  bb. Plant glabrous; fruit glabrous; seeds hairy . . . . . 15. *C. cuyabensis*
aa. Leaves trilobed; petiole > ½ length of lamina . . . . . 16. *C. intermedia*

14. *Cienfuegosia affinis* (H.B.K.) Hochr., Ann. Cons. & Jard. Bot., Genève **6:** 54, 1902.

Hibiscus affinis H.B.K., Nov. Gen. Sp. Pl. **5:** 289, 1821 [Type: inter Angostura et Trapiche de D. F. Farreras (Orinoco): *Humboldt & Bonpland 1076* (P)]. (This location is near the present Ciudad Bolivar; see Sandwith 1925.)

H. sulphureus H.B.K., loc. cit. [Type: Quebrada de Cotecita, Caracas: *Humboldt & Bonpland* 593 (P)] non Wall ex Voigt, Hort. Suburb. Calc. 120, 1845.

Cienfuegosia sulphurea Hassl., Ostenia 343, 1933 (illegitimate, Article 64) non Gareke.

H. sulphureus var. *acutifolius* DC., Prodr. **1:** 451, 1824 [Type: ?].

Fugosia lanceolata Juss. in St.-Hil., Fl. Bras. Mer. **1:** 253, 1825 [Type: Brazil: *St.-Hilaire s.n.* (P)].

F. affinis Juss. in St.-Hil., loc. cit. [Type: Brazil: *St. Hilaire s.n.* (Holotype: P, isotype: P)].

Hibiscus hilairei Kuntze, Rev. Gen. Pl. **1:** 69, 1891 (as *H. Hilairii*).

Fugosia phlomidifolia Juss. in St.-Hil., Fl. Bras. Mer. **1:** 253, 1825 [Type: Brazil, in campis prope vicum Chapada in parte provinciae Minas Geraës dicta Minas Novas: *St.-Hilaire s.n.* (Holotype: P, isotypes: F, P)].

Cienfuegosia phlomidifolia Garcke, Bonpl. **8:** 150, 1860.

Hibiscus phlomidifolia Kuntze, Rev. Gen. Pl. **1:** 69, 1891.

Fugosia campestris Benth. ex Hook., Jour. Bot. **4:** 120, 1842 [Type: British Guiana: dry savannahs, Rio Branco: *Schomburgk* 838, July 1840 (1839?) (Isotypes: BM, F, FI, G, GH, L-2 sheets, NY, OXF, P (photo-MO), US)].

Hibiscus campestris Kuntze, Rev. Gen. Pl. **1**: 69, 1891.
Cienfuegosia affinis var. *campestris* Hochr., Ann. Cons. & Jard. Bot. Genève **6**: 54, 1902.
Fugosia guianensis Klotzsch ex Schomb., Reise Brit. Guiana **3**: 1171, 1848 [Type: Auf der Savanne an der Mündung des Pirara, *Schomburgk s.n.* (K-?)].
F. retusa Turcz., Bull. Soc. Nat. Mosc. **31**: 197, 1858 [Type: Venezuela: prov. Cumanensis, prope Guanaguana, alt 2000 ped, Mar. 1846, *Funck & Schlim 700* (Isotypes: G, LD, LE, W as photo MO)].
Cienfuegosia phlomidifolia var. *humilis* Gürke in Mart., Fl. Bras., **12**(3): 575, 1892 [Type: *Funck & Schlim 700*] (illegitimate, Article 63).
Cienfuegosia affinis var. *humilis* Hochr., Ann. Cons. Jard. Bot., Genève **6**: 54, 1902 (illegitimate, Article 63).
C. riedelii Gürke in Mart., Fl. Bras. **12**(3): 576, 1892 [Type: in campis siccis prope Rio Pardo, Sept 1826, *Riedel 543* (Type: LE)].
Hibiscus rectiflorus Rusby, Mem. N.Y. Bot. Gard. **7**: 300, 1927 [Type: Bolivia: near Reyes, 24 Oct 1921, *White 1538* (Holotype: NY, isotype US)].
Illustrations: Fig. 21, a-e; also St.-Hilaire (op. cit.) t. 50; Schumann (1890) fig. 20 I.; Martius (1892) Pl. 112, fig. 1, Pl. 113, fig. 1; Szumkowski (1952) Fig. 1-6; (1953) Fig. 2-6; Fryxell (1968) Fig. 3,f.

Upright shrub, 1 to 6 or more feet high. Stems woody, densely pubescent (though pubescence sometimes absent on lush regrowth and often lost on old woody branches), terete, punctate. Leaves ovate to elliptic, entire, penninerved (veins prominent below), acute, sometimes obtuse, 3-12 cm long, about ½ as broad (rarely narrower), rarely glabrate, generally weakly pubescent to glabrous above and densely to moderately pubescent below (young growth often yellowish-canescent), punctate. Petioles 1-15 mm (approximately 1/10 length of lamina or less, the leaves sometimes subsessile), punctate, usually pubescent. Stipules filiform, pubescent, 3-10 mm, early-caducous. Peduncle axillary, solitary or sometimes multiple, unjointed or sometimes articulate, punctate, pubescent, 1-8 cm. Involucel of 8-10 bractlets; bractlets linear-lanceolate to sub-spatulate, pubescent, punctate (punctae often obscured by pubescence), 8-22 mm (nearly equaling calyx, persistent. Calyx 1-2½ cm, punctae 1/10 mm diam., often obscured by pubescence, densely to moderately pubescent; lobes 3-ribbed. Petals 2½-5 cm, yellow with maroon spot on claw having yellow radii. Androecium maroon throughout, punctate; anther mass obovate. Style pallid, punctate, greatly exceeding androecium (sometimes equaling petals); stigma 3-4-lobed, dark-red, pubescent. Fruit 3-4-valved, punctate, 1-1½ cm, ovoid, densely ascending-villous without (hairs 1-2 mm). Seeds turbinate to sub-globose, 2-3 mm, sub-glabrous (covered with very short, sparse, rusty hairs). Embryo epunctate. Chromosome number: $n = 10$.
Vernacular names: In Venezuela *C. affinis* is known as *"algodon de sabana"* (cotton of the savanna). In Brazil the names *"algodão do campo"* (field cotton) and *"algodão bravo"* (wild cotton) have been recorded.

This species occupies a key position to our understanding of the subg. *Cienfuegosia*. It is herein interpreted as the most primitive species on the basis of its morphology. At the same time a remarkably clear transitional series connects this species directly with the more specialized representatives of sect. *Cienfuegosia*.

This plant is remarkably plastic in phenotype when grown in culture. Comparison of field-grown and greenhouse plants (the latter receiving partial shade and few temperature extremes) indicates that leaf shape, leaf size, petiole length,

amount of pubescence, and articulation of the peduncle are among the traits affected. Seasonal changes (temperature and/or photoperiod) have similar effects. Much of the considerable variation encountered in herbarium collections of this species is probably caused by ecologic (or seasonal) differences and does not represent genetic or taxonomic diversity, although ecotypic variation may exist as well. I therefore feel justified in presenting so rich a synonymy for a single variable taxon.

For example, the long-petioled glabrate phenotype that characterizes the holotype of *Fugosia lanceolata* (and also *Woronow 7528*) is similar to the phenotype of *Cienfuegosia affinis* growing in culture in its early flush of spring growth (cf. *Fryxell 15016* and *15011*). This same plant, during the balance of the growing season, develops the short petioles and dense pubescence that are typical of *C. affinis*. Thus, the type of *F. lanceolata* can confidently be assigned to *C. affinis* on the basis of its sericeous capsule and subglabrous seeds. The type of *C. riedelii* is an exceptionally tomentose specimen, but appears to differ in no other respect.

Perhaps more than one taxon exists within this group. If so, only the comparative culture of a wide range of material could demonstrate their existence.

The flowering response of *C. affinis* is under strong photoperiodic control when plants grow under conditions of fluctuating daylength (i.e., at higher latitude). *C. affinis* is distributed from approximately 10° N latitude to about 22° S latitude. Over the greater part of this area daylength does not vary significantly through the course of the year. Collation of collection dates of flowering specimens shows that this plant flowers in the field more or less throughout the year. When cultivated at higher latitudes, however, it flowers only under short-day conditions. At Tempe, Arizona (33° N latitude), for example, it flowers only from November through April and is completely vegetative during the summer months.

Distribution (Fig. 11): Venezuela and adjoining parts of Colombia; Brazil: Rio Branco (and in adjacent British Guiana), Ceara, Bahia, Minas Geraes, Goias, and Mato Grosso (and in adjacent parts of Paraguay and Bolivia). Szumkowski (1953) discussed the ecological and geographical distribution of *C. affinis* in the Venezuelan part of its range. His map (loc. cit., p. 6) does not indicate the complete distribution of the species in Venezuela, but only the locations where he made routine field observations on a seasonal basis. Szumkowski's field observations showed that the plant is widespread and abundant in the chaparral zone of Venezuela, and occurs primarily along the eastern slopes of the Cordillera de Merida (at altitudes up to 1100 m) and northeast to the coast in the vicinity of Caracas and Cumaná. It is also abundant in the plains that border the chaparral zone to the southeast (at an altitude of 100-200 m) in the states of Barinas and Portuguesa. The species apparently occurs under similar (chaparral and savanna) ecological conditions throughout its range.

COLOMBIA: *Moritz 98* (G, LE); *Wagener 350* (UC).

VENEZUELA: Cumaná, S. Antonio, *Funck 181* (BM, G, LE, P); Cocollar, *Funck & Schlim 700* [G, LD, LE, MO (as photo of W)]. MIRANDA: S slope of La Silla above Los Palos Grandes (Caracas), ca 1100 m, *Dennis 2278* (K); thickets on roadsides, betw Turmero and Ocumare del Tuy, alt 1000 m, *Williams 13585* (F). ARAGUA: prope Coloniam Tovar, *Fendler 105* (BR, G, GH, K, NY, US), *106* (GH). DISTRITO FEDERAL: Caracas, *Elias 183* (F), *223* (F), *398* (F), *Tatavinow s.n.* (LE), *van Landsberge 249* (L); in savan-

nas, Lower Cotiza (Agr. Exp. St.), *Pittier 8143* (MO, UC), *Warming s.n.*, 11 Jan 1892 (C); Quebrada de Cotecita, *Humboldt & Bonpland 593* (P), *Curran & Haman 1072* (GH), *de Grosourdy s.n.*, 1864 (P); thickets on side of rd to Baruta, alt 1000 m, *Williams 13646* (F), *Steyermark 55189* (F, NY); Trapiche de D. F. Farreras, *Humboldt & Bonpland 1076* (P). CARABOBO: Llanos de S. Carlos, *Linden 1456* (BM, BR, G, GH, LE, OXF), *Warming 442* (C); Valencia, *Warming s.n.*, 29 Dec 1891 (C), *Eggers 13560* (C); Mariara, *Mocquerys 960* (P); Llano de la Puerta, *Woronow 7528* (LE).

BRAZIL: CEARA: *Gardner 1459* (FI, G, GH, NY, OXF, P). RIO BRANCO: Boâ Vista cume do serrote Murupuzinho, *Ducke 2068* (IAN, R); Serra de Pracaieá, Surumú, *Ule 7979* (K, L); terreno pedregoso, Serra do Quixada, Contâo, Rio Cotingo, *Silva 144* (MG, TAES). GOIAS: entre ——————— et Conte Savaido *Glaziou 20714* (BR, G, K, P), *Weddell 2641* (P). MINAS GERAIS: Lagoa Santa, na Serra de Santa, *da Costa 27A* (R), *Martius 2681* (M); in campis ad Contendar, *Martius 2680* (M); in sepibus ad Columbi praed. Serro Frio, *Martius 1397 (2678)* (M); Riacho das Varas, *Glaziou 18882* (C, P, R), *Claussen 374* (BR), *549* (G), *950* (FI); Cons. Matta, Rodeador, *Brade 13440* (B); Ituitabá, *Macedo 372* (US), *4197* (US); Minas Novas, *St.-Hilaire 1021* (F, MO (as photo), P), *St.-Hilaire s.n.* (Holotype of *Fugosia affinis* St.-Hilaire, P), *St.-Hilaire s.n.* (Holotype of *Fugosia lanceolata* St.-Hilaire, P). MATO GROSSO: Tapirapoan, *Hoehne 1679* (R); Coxipó de Ponte, Cuyabá, *Hoehne 4615* (R), *3000* (R); St. Luiz de Cáceres, *Hoehne 198* (R), *Landeman 2094* (K, OXF); Lava-pes Cáceres, *Hoehne 171* (R); ad Rio Coxim, *Riedel s.n.* (OXF); in campis siccis, Rio Pardo, *Riedel 543* (LE); Cuyabá, *Malme s.n.*, 17 Jun 1902 (S); 40 km N de Cuiabá, Rio Mirini, *Gregory et al. 9908* (LH, TAES); Esmeril, *Lindman A3037* (S); nr source of Rio Paraguay, betw Rio Amolar and Rio Nobres, 1500 ft, *Smith 253* (K), *Gaudichaud 44* (P), *Raben 886* (BR); Itú, *Riedel 2024* (GH, K, LE, P, US, Z); Oeiras, N Brazil, *Jobert 1037* (P), *Burchell 5620* (K), *Pohl 223* (M).

BRITISH GUIANA: Roraima, *Schomburgk 415* (BM, G, OXF); dry savannas on Rio Branco, *Schomburgk 838* (BM, F, FI, G, GH, L, MO (as photo), NY, OXF, P, US); Limao (Mt. Roraima and vicinity), *Tate 99* (NY); Rupununi Distr., Massara and Good Hope, *Graham 248* (K).

PARAGUAY: Campo medio bajo Esperanza, in altaplanitie et declivibus "Sierra de Amambay," *Hassler 10706* (C, G, K, MICH, MO, NY, P, S, UC, US); in campis in regione cursus superioris fluminis Apa, *Hassler 8219* [B (photo in MO), C, G, GH, MICH, MO, NY, P, S, UC, US].

BOLIVIA: 200 m, *Velasco 7* (NY), *Jeullet 727* (Juillet ?) (P); Reyes, *White 1538* (NY).

IN CULTIVATION: (provenance: Maracay, Venezuela) *Fryxell 15011* (ARIZ, TAES), *15016* (TAES).

15. *Cienfuegosia cuyabensis* Pilger, Engl. Bot. Jahrb. **30:** 171, 1902 [Type: Brazil, Mattogrosso: im Serrado bei Cuyabá, kriechend an trockenen, freien, sandigen Stellen, die Zweige dem Boden anliegend: *Pilger 289*, Mar 1899 (Holotype: B†, photo in MO); neotype: Brazil, Mato Grosso: Cuyabá, *Malme 1666*, 9 June 1902 (S)].

Illustrations: None.

Decumbent to ascending perennial subshrub. Stems slender, woody, glabrous, minutely but abundantly punctate, weakly ridged and greenish when young. Leaves narrowly elliptic, entire, acute, punctate, glabrous, penninerved (midrib prominent below), 3-6 cm long, 10-17 mm wide, 3-4 times as long as broad. Petioles 1-6 mm, glabrous. Stipules linear, ciliate, inconspicuous. Peduncles 1-3 cm long, glabrous, ridged. Involucel of 9-10 bractlets; bractlets linear (sometimes sub-spatulate), acute, glabrous, punctate, 1-nerved, 7-10 mm long, < 1 mm wide. Calyx 10-12 mm, glabrous; lobes acute, 3-ribbed; intercostal areas scarious. Petals 3-3½ cm, punctae translucent, yellow with maroon spot having yellow radii. Androecium maroon, anther mass obovate. Style elongate, nearly equaling petals,

undivided, pallid, punctate. Stigma dark-red. Fruit glabrous within and without, tuberculate, epunctate (?), ovoid, 8-10 mm. Seeds hairy; hairs tan.

The holotype of *Cienfuegosia cuyabensis* was apparently also among those lost from the Berlin herbarium, although a photograph of the holotype is preserved in the herbarium of the Missouri Botanic Garden. No isotypes of this species are known and no other specimens were cited by Pilger. Therefore, it is necessary to designate a neotype. *Malme 1666* is the only specimen available. Fortunately, it is an excellent one and conforms closely to Pilger's detailed description.

Distribution (Fig. 11): Brazil: Mato Grosso: apparently restricted to region around Cuyabá. Malme, however, notes it to be "not uncommon." His field notes state (translation from note attached to Stockholm specimen cited below): "In hills on somewhat open, somewhat moist localities, not uncommon but by this time [i.e., June] almost bloomed out. Of ± prostrate to commonly upright habit." Ulbrich (1914) states that this species also occurs in Bolivia, but I have found no evidence to support this assertion.

BRAZIL: MATO GROSSO: Cuyabá, *Malme 1666* (S); im Serrado, kriechend an trockenen, freien, sandigen Stellen, die Zweige dem Boden anliegend, *Pilger 289* (B†, photo in MO).

16. *Cienfuegosia intermedia* Fryx., Britt. **19:** 37, 1967 [Type: Mexico, with illegible label, and added number Herb. Lugd. Bat. No. 908, 140-849 (Holotype: L)].

Illustrations: none.

Low, herbaceous perennial arising from a woody rootstock. Stems weakly angled, punctate, glabrate. Leaves 3-lobed, 1½-2 cm long, about as broad; lobes oblong to obovate, sometimes constricted at base, obtuse to apically 3-dentate, glabrate above, ciliate-margined, punctate and sparsely scabrous below on veins. Petioles 10-12 mm, canaliculate, punctate, pubescent near juncture with lamina. Stipules 3-5 mm long, 1 mm broad, lanceolate, punctate, 1-nerved, ciliate, caducous. Peduncles 1½-3½ cm (exceeding leaves), axillary, solitary, not articulate, angled, punctate, sparingly pubescent (hairs stellate, 0.1-0.2 mm). Involucels of ca 10 bractlets, nearly equaling calyx; bractlets 8-10 mm long, < 1 mm broad, lanceolate, ciliate, punctate. Calyx deeply lobed, 10-12 mm, scabrous-ciliate on margins and veins, otherwise glabrate, lobes 3-ribbed, lanceolate, acuminate. Petals 2 cm, punctate, yellow with dark spot at base. Staminal column pallid; anther mass oblate. Style simple, punctate, nearly equaling petals; stigma red. Fruits unknown.

Distribution: In addition to the word "Mexico" and the number "2," the label on the holotype also bears the word "Mendes," which may refer either to the collector or to a locality.

MEXICO: (illegible label) (L-holotype).

6. SECT. **Paraguayana** Fryxell, sect. nov.

Folia simplicia vel exigua lobata, integra vel dentata. Stipulae subulatae. Involucrum 8-10 phyllum; foliolia involucrorum calycem subaequantia. Nectaria involucrorum et foliorum nulla. Petala epunctata. Capsulae glabrae intus.

Plant decumbent to ascending, herbaceous to semi-woody, arising from perennial rootstocks, glaucous to pubescent, minutely punctate. Leaves entire to weakly lobed and dentate, rotund to elliptic or obovate. Stipules symmetrical, subulate. Flowers axillary, solitary, on unjointed peduncles. Involucral nectaries lacking. Involucel of 8-10 bractlets; bractlets prominent, distinct, not grouped, linear-lanceolate to spatulate. Calyx punctate, glabrate, pubescent, or scabrous; lobes acute to acuminate. Petals epunctate, yellow, with or without dark spot on claw; spot when present sometimes having yellow radii. Style single or slightly divided apically. Stigmas capitate. Fruits glabrous or densely villous without, glabrous within.

Type species: The type of sect. *Paraguayana* is *Cienfuegosia sulfurea* (Juss.) Garcke. The name of this section is chosen to emphasize the importance of Paraguay as a focal point of the distribution of *Cienfuegosia* as a whole, and of this section of the genus in particular. All four species of sect. *Paraguayana* occur in Paraguay; two of them are endemic to Paraguay.

Key to Species of Section Paraguayana

a. Leaves dentate, minutely puberulent to pubescent.
  b. Foliage notably pubescent; leaves moderately dentate, as broad as long; seed hairs loosely appressed; calyx margin (and leaf margin) densely ciliate (hairs ½-1 mm); style divided apically; stigmatic lobes 3-4, distinct, light-colored; fruit 3-4-celled ..... 17. *C. sulfurea*
  bb. Foliage sparsely scurfy-puberulent becoming glabrate; leaves coarsely serrate, longer than broad; seed hairs tightly appressed (seeds appearing hairless); calyx margin not or scarcely ciliate; style undivided; stigma dark-red, 4-5-lobed; fruit 4-5-celled ..... 18. *C. drummondii*
aa. Leaves entire, glabrous.
  c. Leaves glaucous, obovate, apiculate, primarily 3-nerved; stipules persistent, often equaling petioles; pedicels long (> 5 cm); calyx and involucel nearly glabrous; fruit glabrous; petioles 1/10 ¼ length of lamina..... 19. *C. integrifolia*
  cc. Leaves orbicular to ovate, 5-nerved; stipules caducous, inconspicuous; pedicels short (1-4 cm); calyx and involucel scabrous; fruit ascending-sericeous; petioles about ½ length of lamina ..... 20. *C. subprostrata*

17. *Cienfuegosia sulfurea* (Juss.) Garcke, Bonpl. **8:** 150, 1860 (as *C. sulphurea*) non (H.B.K.) Hassl., Ostenia 343 (1933).

Fugosia sulfurea Juss. in St.-Hil., Fl. Bras. Mer. **1:** 252, 1825 [Type: Uruguay: paturage seca prés le village de S. Salvador, province Cisplatina, *St.-Hilaire 241* (Holotype: P, isotype: P)].

Hibiscus Jussieui Kuntze, Rev. Gen. Pl. **1:** 69, 1891 (based on *Fugosia sulfurea* Juss.).

Cienfuegosia sulphurea var. *genuina* Gürke in Mart., Fl. Bras. **12**(3): 577, 1892 (illegitimate, Article 26).

C. drummondii (A. Gray) Lewt. emend. Hassl., Ostenia 342, 1933 pro parte (illegitimate, Article 67).

C. drummondii var. *pubescens* Hassl., loc. cit. 343. [Types: prope Fray Bentos: *Arechavaleta 1524* (MVM? -n.v.), and *Sellow 1053* (?) syntypes].

Even though the combination *C. drummondii* (A. Gray) Lewt. emend. Hassl. is in contravention of Article 67, in that Hassler did not adopt the earlier epithet *sulfurea* from Jussieu [as Robinson (1895) had done earlier in combining these taxa], nevertheless the varietal epithet *pubescens* must be accepted as valid under the provisions of Article 68.

Illustrations: Fig. 22, e-h; also St.-Hilaire (op. cit.) Pl. 49; Rodrigo (1941) Fig. 2; Fryxell (1968) Fig. 3,k.

Procumbent perennial herb arising from woody root-stock, canescent on young growth. Stems terete to weakly ridged, densely hirsute (becoming glabrate in age), minutely punctate. Leaves orbicular to reniform, sometimes weakly 3-lobed, dentate to crenate, cordate to truncate, obtuse (or sometimes acute), 3-5-nerved, as broad as or broader than long, hirsute below, sparingly hirsute to glabrate above (hairs ½-1 mm), densely ciliate-margined. Petioles pubescent (especially near juncture with lamina), punctate, ½ length of lamina or less. Stipules narrowly subulate, acute to acuminate, punctate, pubescent below, glabrous above, ciliate on margin, 1-4 mm. Peduncles pubescent, 1-5 cm, punctate. Involucel of ca 9 bractlets; bractlets hirsute (especially on margin), lanceolate to spatulate, acute, 5-10 mm long, 1-2 mm broad, 1-nerved, punctate. Calyx 10-15 mm, exceeding involucel, hirsute without, glabrous within, sometimes costulate; lobes broadly ovate, acute, 3-veined, densely ciliate (hairs ½-1 mm) on margins. Petals 1-2½ cm, yellow (sometimes turning blue-green in sicco), lacking basal petal spot or sometimes with vestigial spot. Androecium white (sometimes reddish in sicco), epunctate; anther mass obovate; stamens 5-ranked; anthers yellow. Style greenish-white, sometimes punctate, often slightly 3-4-parted apically; stigmatic lobes 3 to 4, usually free, light red. Fruit glabrous within and without, minutely punctate, 3-4-valved, 5-10 mm, globose. Seeds ca 4 mm, turbinate, comose; seed hairs tan to red-brown, appressed, 5-7 mm long. Embryo epunctate. Chromosome number: $n = 10$.

The original spelling of the specific epithet, *sulfurea*, was altered by Garcke to *sulphurea,* and his orthographic change has been perpetuated by most subsequent authors. The original spelling is here restored.

The flowers of this species sometimes develop cleistogamically, (cf. Fryxell, 1963).

Distribution (Fig. 14): Argentina: northwestern Córdoba, Santa Fé, Entre Ríos, Corrientes, and eastern Chaco; Uruguay: extreme western portion; Paraguay; in Río Paraguay valley. The trailing stems of this species form carpets over the ground in dry scrub and in moist meadows. It occurs both on heavy clay soils and on sand. In Entre Ríos and Chaco it is sympatric with *C. drummondii* and apparently occurs in mixed populations with it, as is attested to by several mixed collections *(Lorentz 1428, Aguilar 1171, Krapovickas 7971, Schulz 169,* and *Molfino & Clos s.n.)* that have been made. In spite of such confusion, however, the two species can be easily distinguished (see accompanying key, p. 221, and that given by Rodrigo, 1941), do not intergrade in nature, and hybridize in culture only with difficulty. The hybrids are lethal at an early age (Palacios & Tiranti, 1966). Another mixed collection from Corrientes *(Schwarz 9949)* indicates that *C. sulfurea* also occurs together with *C. ulmifolia.*

Paraguay: in arenosis pr. Concepción, *Hassler 7315* (BM, G, K, MO, NY, P, S, UC); San Salvador, *Rojas 2592* (M, G); Prov. Pilar, Curuparitz, *Schulz 7978,* (LIL).

Argentina: chaco: Dpto. Resistencia: Colonia Benitez, *Schulz 169* (BAB-p.p.), *627* (S); Margarita Belén, *Aguilar 640* (LIL), *1037* (LIL), *1171* (LIL-p.p.), *Meyer 2653* (LIL); Campo de Tajamar, *Schroeter 37* (BAB). corrientes: Dpto. Curuzú Cuatiá: *Spegazzini s.n. (149?),* 2-4 Apr 1940 (BAB), park-like country on heavy clay, Ruta 14, ca Km 625, *Pedersen 4698* (BR, C, US), Perugorria, *Cabrera 10572* (LIL, M), *Ibarrola 2556* (LIL), *2263* (BAB, LIL); al norte de Sauce, *Castellanos 34437* (BA). Dpto.

Mburucuyá: Estancia "Santa Maria," *Pedersen* 5283 (C, P, S,). Dpto. San Cosme: Paso de la Patria, Costa Toledo, 55 m, *Meyer* 8792 (LIL). Dpto. Capital: Santa Catalina, *Ibarrola* 944 (LIL), *Malvarez* 1473 (LIL), *Hicken s.n.*, 26 Mar 1902 (SI), *d'Orbigny* 86 (P), *Ibarrola* 2668 (LIL), *Dupre s.n.* (P), *Com. Escuela del Centenario* 78 (BA). Dpto. Mercedes: *Spegazzini s.n. (69?)*, 23-31 Mar 1940 (BAB), Justino Solari cercanias, *Ibarrola* 2607 (SI), Camino de la Feria, *Rodrigo* 606 (NY). Dpto. Empedrado: *Schwarz* 9949 (LIL-p.p.), El Sombrero, *Schwarz* 10084 (LIL). Dpto. Monte Caseros: Mocoreta cercanias, *Ibarrola* 2423 (LIL). Dpto. San Martín: en bosque de Quebracho Blanco, Nandubay 5 km N de Pellegrini, *Krapovickas* 7956 (LIL), entre Mercedes y Pellegrini, en monte de Nandubay y espinillos, *Krapovickas* 7961 (LIL); Bella Vista, *Rojas Acosta s.n.*, Oct 1904 (BAB). SANTA FE: Dpto. San Cristóbal: Estacion Hersilia, *Muniez s.n.*, 25 Jan 1907 (BAB), *Balegno* 612 (LIL). ENTRE RIOS: Dpto. Concordia: Federal, *Molfino & Clos s.n.*, 31 Mar 1927 (BAB-p.p.) *L. H. s.n.*, 15 Feb 1917 (BA), Federación, *Crovetto & Piccinini* 4701 (BAB), *Crovetto & Leguizamón* 4913 (BAB, TAES). Dpto. La Paz: *Lorentz* 1428 (UC-p.p.), Sauce de Luna, *Krapovickas* 7971 (LIL, SI-p.p.); Colón, *Meyer* 10595 (LIL), *Castellanos* 1168 (BA); Gualeguaychú, *Jurado* 15 *bis* (SI), *Garcia s.n.*, 17 Jan 1943 (LIL); Pehuajo Norte, *Serié & Mijoya* 665 (BA); Concepcion del Uruguay, *Lorentz* 883 (BM, FI, G, GH, L, LE, M, OXF, P, UC, Z), 571 (UC), 253 (UC), *s.n.*, April 1880 (P), *s.n.*, 3 May 1880 (CORD), *Schulz* 305 (LIL), *Baez* 75 (BA); Picada, *Naboulet* 164 (BA); Villaguay, *Meyer* 11273 (LIL), *Müsch* 995 (GH). CORDOBA: Rio Tercero, Estancia, *Stuckert* 9679 (CORD, G, S), 10042 (G, S); Rio Primero, Estancia "San Teodoro," *Stuckert* 11558 (CORD, G), 21440 (CORD, G, TAES); San Justo, Sacanta, *Stuckert* 7081 (G), 9940 (G, S).

URUGUAY: Entre Belén y Bella Unión, *Ragonere & Piccinini* 6554 (BAB, TAES); Paturage seca prés le village de S. Salvador, Provincia Cisplantina, *St.-Hilaire* 241 (P); Manatial cerca de Mercedes, *Castellanos s.n.*, 23 Jan 1947 (LIL); cerca de Bella Union, *Castellanos s.n.*, 28 Mar 1948 (LIL); Nera (Soriano), *Berro* 1466 (G); Salto, *Osten* 5407 (US); Fray Bentos, *Fruchard s.n.*, 29 Jan 1879 (1899?) (P).

IN CULTIVATION: (provenance: Colonia Benitez, Chaco, Argentina) *Fryxell* 15007 (ARIZ, TAES).

18. *Cienfuegosia drummondii* (A. Gray) Lewt., Bull. Torr. Bot. Club **37:** 473, 1910.

Fugosia drummondii A. Gray, Pl. Wright. **1:** 23, 1852 [Type: Gonzales, Texas: *Drummond* 42, 1834 (Holotype: K, isotypes: BM, GH, LE, OXF, P)].

Hibiscus drummondii Kuntze, Rev. Gen. Pl. **1:** 69, 1891 non Turcz. Bull. Soc. Nat. Mosc. **31:** 195, 1858.

Cienfuegosia sulphurea Garcke emend. Robins. in Gray & Robins., Syn. Fl. N.A. **1**(1): 337, 1895 pro parte.

C. sulphurea var. *drummondii* Hochr., Ann. Cons. Jard. Bot., Genève **4:** 173, 1900.

Elidurandia texana Buckl., Proc. Acad. Sci. Philad. **1861:** 450, 1862 [Type: Texas: on the banks of the Colorado River above Austin, *Buckley s.n.*, May-June 1861 (PH)].

Hibiscus pulverulentus Griseb., Abh. Königlich. Ges. Wiss. Gött. **24:** 49, 1879 [Type: Argentina: Salta: *Lorentz & Hieronymus* 1082, Nov 1873 (Holotype: GOET, isotype: UC)].

Fugosia pulverulenta Hochr., Ann. Cons. Jard. Bot. Genève **4:** 173, 1900.

Cienfuegosia sulphurea var. *glabra* Gürke in Mart., Fl. Bras. **12** 3): 577, 1892 [Type: *Lorentz & Hieronymus* 1082].

C. sulphurea var. *glabra* f. *intermedia* Chod. & Hassl., Bull. Herb. Boiss., ser. 2, **5:** 302, 1905 [Type: Paraguay: in arenosis prope Concepción, Sep 1901, *Hassler* 7315*b* (G)].

C. sulphurea var. *major* Hassl., Repert. Spec. Nov. **7:** 379, 1909 [Types: Paraguay: Gran Chaco, ad ripam occidentalum flum. Paraguay, latit. S. 22° 21′-23° 30′, Oct 1903, *Hassler* 2416 (Lectotype: G- Herb. Delessert, isotypes: G, GH, NY, P, S, UC); *Rojas* 100 (Syntype: G)].

C. drummondii var. *genuina* Hassl., Ostenia 343, 1933 (illegitimate, Article 26).

Fugosia sulphurea var. *trifida* Griseb. ex Rodrigo, Darwiniana **5:** 220, 1941 nomen nudum.

Although the type of *Hibiscus pulverulentus* Grisb. was cited by Gürke in publishing *Cienfuegosia sulphurea* var. *glabra* Gürke, the latter epithet cannot be rejected under Article 63 as nomenclaturally superfluous, but must be retained as

legitimate since it is of different rank. The two names are, of course, synonymous, since they are based on the same material.

Illustrations: Fig. 22, a-d; also Smith (1895) Pl. 49; Seckt (1929-1930) Pl. 13, Fig. 370; Rodrigo (1941) Fig. 3, C & D; Fryxell (1963) Fig. 1, a & b, (1968) Fig. 3,j.

Perennial herb or subshrub, arising from woody rootstock. Stems semi-decumbent to ascending, angled, sparsely puberulent to glabrate, minutely punctate. Leaves coriaceous, ovate to elliptic, sometimes weakly 3-lobed, coarsely serrate to denticulate (rarely subentire), glabrate (margin not or scarcely ciliate), minutely punctate, about 1½ times as long as broad, truncate, acute. Petioles ½ length of lamina or less, minutely puberulent near juncture with lamina or glabrate throughout, triquetrous, punctate. Stipules subulate or lanceolate, 1-8 mm long, ½-1 mm broad, punctate, caducous, glabrate to ciliate-margined, acute to acuminate. Peduncles sparingly puberulent to glabrate, 2-11 cm, punctate. Involucel of 8-10 bractlets; bractlets lanceolate to spatulate, 6-14 mm long, 1-nerved, acute to acuminate, punctate, minutely puberulent or glabrate (rarely setose), 1-2 mm broad. Calyx 10-20 mm, exceeding involucel, inconspicuously punctate, minutely puberulent or glabrate (rarely setose), sometimes weakly costulate; lobes lanceolate, acute to acuminate, 3-nerved, rarely sparingly ciliate-margined, sometimes laciniately divided into 2 or 3 teeth. Petals 1½-3½ cm, yellow (sometimes turning blue-green in sicco), with solid dark-red basal petal spot, or with petal spot lacking. Androecium epunctate, whitish (or dark-red if petal spot is present); anther mass obovate; stamens 5-ranked; pollen yellow. Style greenish-white, punctate; stigma 4-5-lobed, dark-red. Fruit glabrous within and without, minutely (and sometimes obscurely) punctate, 4-5-valved, obovoid-obtuse (sometimes ovoid-rostrate), 8-14 mm. Seeds angularly turbinate, tan, 3-4 mm; seed hairs tightly appressed (seeds appearing hairless). Embryo epunctate. Chromosome number: $n = 10$.

Hochreutiner (loc. cit.) noted that Grisebach's *Hibiscus pulverulentus* belongs in *Fugosia* (i.e., *Cienfuegosia*) but did not consider the problem beyond making the new combination. Kearney (1953) independently made the same observation, noting the existence of the UC isotype, but he identified the plant as *C. sulphurea* (St.-Hil.) Garcke on the basis of the keys of Rodrigo (1941) and Hutchinson (1947). I have examined this specimen, as well as the holotype (GOET), and it unquestionably belongs in *C. drummondii,* not in *C. sulphurea.* These two species are not distinguished by Hutchinson, but are clearly distinguished by Rodrigo.

Three vernacular names and three medicinal uses for this species are on record. Seckt (1929-30) records the name *"mercurio"* for what is apparently (on the basis of his illustration) this species, although he identifies it as *C. sulphurea* (St.-Hil.) Garcke. On *Escobar 13* (BAB) from the province of Chaco the same name is recorded, together with the information that "la medicina lugareña la utiliza como purgante." On a specimen from Colonia Benitez, Chaco, without indication of collector or date (BAB), the name *"yerba del indio"* is recorded together with the statement "para llagas gargarismo." On *Rojas 13589* and *Pier-*

rotti 1 the name *"guaicurú caá"* is given together with the indication that the plant is used as an astringent. This name is evidently in the guaraní language (Cadogan, 1957) and may best be translated as "plant of the Guaicurú Indians," a name comparable to the spanish *"yerba del indio."* In none of these cases is the part of the plant used for these medicinal purposes given.

This species is polymorphic for petal spot and pigmentation of the androecial column, these two traits simply being two expressions of the same condition. This variation is assumed to have a simple genetic basis and little or no taxonomic significance. Mixed populations apparently occur, judging from mixed collections that I have seen, e.g., *Lindman A2235* (S).

Distinctive features of this species include the tendency to develop divided calyx lobes, which are notable in *Venturi 551* (SI) for example, and the 4-5-lobed stigma and 4-5-valved capsule, that are in contrast to the basically trimerous condition found generally in the remainder of the genus.

Distribution (Fig. 12 and 12a): Argentina: Salta, Tucumán, Santiago del Estero, eastern Chaco and Formosa, Corrientes, Santa Fé, Entre Rios, and Córdoba; central Paraguay; Brazil: southernmost Mato Grosso in the vicinity of the Rio Apa; United States: Texas, in a narrow belt from Brownsville north to Austin, being fairly abundant in the vicinity of Corpus Christi. There appears to be no basis for Small's (1933) suggestion that this species may occur on Key West, Florida.

In Argentina *C. drummondii* grows to some extent in mixed populations with *C. sulfurea* and also with *C. ulmifolia*. It is found in low, moist areas with heavy soils that are often saline; its salt-tolerance appears to be high.

Subsequent to the original description of *Fugosia drummondii* and *Elidurandia texana* by Gray and Buckley, respectively, the history of the Texas occurrence of this plant has received considerable attention (Coulter, 1891; Heller, 1895; Smith, 1895; Lewton, 1910; Hanson, 1921; Hutchinson, 1947), and its notably disjunct distribution has been discussed by Bray (1900), Hutchinson (1947), and Fryxell (1967b). The essential facts may be summarized as follows:

Collector	*Locality*	*Date*	*Collector*	*Locality*	*Date*
Drummond	Gonzales	1834	Hanson	Gregory	1919
Buckley	near Austin	ca. 1861	Schulz	Brownsville	1924
Heller	Corpus Christi	1894	Eifrig	Bishop	1925
Nealley	Corpus Christi	1894	Tharp	Woodsboro	1925
Lewton	Taft	1910	Lewton	S. of Dallas	1925

More recent collections [including several seed collections (Lukefahr and Martin, 1962) made available to the author by Dr. M. J. Lukefahr] indicate that the plant occurs commonly, not rarely as reported earlier, in the areas of Brownsville and Corpus Christi. The extension of its range to the north of Corpus Christi (including both type locations) is more problematical, however, since it has not been collected in this area for over 100 years, if one ignores the unsatisfactory designation of locality on Lewton's 1925 collection.

The distributional disjunction shown by *C. drummondii* was probably achieved relatively recently by dispersal from the southern hemisphere to the northern

(Fryxell, 1967b). The time or means of this dispersal are not immediately evident. However, circumstantial evidence suggests that bird dispersal in recent times is a probable explanation. Cruden (1966) and Proctor (1968) discuss the plausibility of birds as plant dispersal agents and note that members of the *Charadriiformes* are likely agents of long-distance dispersal. Proctor emphasizes the capacity of these birds to retain seeds in their crops for long periods, especially seeds in the size range shown by *C. drummondii,* and subsequently to disgorge them intact and thus to disperse them in migration over great distances. Cruden emphasizes the dispersal potential of seeds adhering in mud to the feet and feathers of migrating birds. This explanation is also plausible for *C. drummondii,* since it occurs in moist habitats, although such a means of dispersal lacks force as a general explanation of disjunction since many of the disjunct plant species occur in dry, upland habitats, which the birds do not frequent and where the conditions are not favorable for the adherence of the seeds to the birds. In any case, the latitudinal similiarity of the two portions of the distribution of *C. drummondii* supports the idea that migrating birds are the responsible dispersal agents.

UNITED STATES: TEXAS: Gonzales, *Drummond 42* (BM, GH, K, LE, OXF, P); banks of the Colorado above Austin, *Buckley s.n.* (Holotype of *Elidurandia texana* Buckl.: PH); S of Dallas, *Lewton s.n.,* 25 Aug 1925 (S). Calhoun County: Port Alto, *Drushell 114* (P). Refugio County: *Drushell 176* (P); Woodsboro, Bayside, *Tharp 3606* (TEX, US). San Patricio County: weed in cotton fields, Gregory, *Hanson s.n.,* 7 Jun 1919 (GH, MO); Welder Wildlife Refuge near Sinton, *Tharp s.n.,* 9 Oct 1958 (TEX); roadside, 4 mi NE of Sinton, *Fryxell 701* (TAES); Bishop, *Eifrig 21* (F); slightly saline soil on open bottom, near Sinton, *Wolcott & Barkley 16T416* (F, TEX); 8 mi SW of Taft in swale, *Jones 413* (SMU). Nueces County: 1 mi N of Robstown, *Chapman 3014* (TEX); nr Gardendale, S of Corpus Christi, *Johnston 53175.14* (TEX). Kleberg County: Agua Camp, *Johnston 541181* (SMU, TEX). Corpus Christi: *Heller 1808* (GH, PH, S, UC), *Nealley s.n.,* 1894 (F, LIL, MO). Cameron County: "Victoria" soils area, *Johnston s.n.,* June 1952 (TEX); Brownsville, *Schulz 2969* (F); Laguna Atascosa Wildlife Refuge, *Fryxell 436* (CTES, TAES), *Van Fleet 6095* (TEX); Olmito Rd, near Arroyo Colorado, *Clover 1259* (MICH). Willacy County: among mesquite and cactus, *Shiller M5* (TAES); Sauz Ranch, *Johnston 53175.15* (TEX).

BRAZIL: MATO GROSSO: Porto Murtinho, *Malme s.n.,* 2 Jan 1903 (S), *Robert 887* (BM); Porto Pachico, *Moore 1056* (BM).

PARAGUAY: Chaco, Puerto Casado, *Rojas 1935* (G, M, SI), *Gregory et al. 10601* (LIL), *Lindman A.2235* (S); Puerto Guaraní, campo palmar, *Rojas 13589* (G, LIL, MO, TEX); ad ripam occidentalum flum, Paraguay, *Hassler 2416* (G, GH, K, MO, NY, P, S, UC), *Pride s.n.* (K), *Fiebrig 1233* (G, K, M, S, Z); en face de l'Assomption, *Balansas 1875* (P). CONCEPCION: *Hassler 7315b* (G), *7317* (BM, G); Pilcomayo River, *Morong 929* (BM, GH, MO, NY, PH, US), *Rojas 100* (G); in regione locus Yparacay, Cordillera de Altos, *Hassler 12390* (C, G, GH, K, L, MO, NY, US, Z); ad ripam rivi Igneri, *Hassler 1477* (BM, K, G); von nassem Weisen, Fuerto Olympo, *Ansits 2163* (S); poor saline soil, foot of Cordillera de Villarica, *Jorgensen 3814* (BA, F, GH, LIL, NY, PH, S, SI); Puerte Yatayba, *Daguerie 967* (BA), *Kuntze s.n.,* Nov 1892 (NY).

ARGENTINA: FORMOSA: Dpto. Pilcomayo: Ruta 11 Cda. a Laguna Blanca al km 7, *Morel 2192* (LIL, UC), al km 2, *Morel 2141* (GH, LIL); Ruta 86 al S. O. a 36 km de Puente Gobernacia, *Morel 2756* (LIL, MO); al E de Puerto Porteña a 2 km, *Morel 2388* (LIL); Ruta 11 Clorinda a Formosa km 4, *Morel 1684* (LIL); camino de Clorinda a Paraiso, *Rojas 8975* (SI). Dpto. Pirané: Pilagá, *Morel 734* (LIL, US), *33* (GH, LIL), *Pierotti 4226* (LIL), *4268* (LIL); Casco Cué, *Morel 896* (LIL, NY); Guayacan (20 km al noroeste de Pirané), *Pierotti 6* (LIL, SI); Estero Grande, *Reales 63* (LIL); Estancia Lacoré, *Pierotti 1* (LIL); Laguna de los Rios, *Reales 73* (LIL); Monteagudo, *Reales 172* (LIL). Dpto. Clorinda: Curema, *Reales 312* (LIL). Dpto. Patino: Las Lomitas FCE, *Krapovickas 1293* (LIL), *1305* (LIL). Dpto. Formosa: 10 km de la ciudad, sobre ruta 11 al N, *Krapovickas 992* (LIL), *Jorgensen 3054* (BA, MO), *Kermes 282* (BAB, TAES). CHACO: Dpto.

Resistencia: Colonia Benitez, *Schulz 169* (BAB-p.p.); Margarita Belén, *Aguilar 1263* (LIL), *1171* (LIL-p.p.). Dpto. Florencia: La Sabana, *Basaldua s.n.*, Oct 1904 (BAB). Dpto. Nopalpí: Las Cuchillas (Lote F), *Buratovich 338* (LIL); La Clotilde de P. R. Sáenz Peña, *Buratovich 284* (LIL), *Baez 12* (BAB); Rio Bermejo, Rosario del Dorado, *Flossdorf s.n.*, 27 Aug 1906 (BAB); Sección 17, *Flossdorf s.n.*, 28 Nov 1906 (BAB, TAES); Fontana, en suelos arcillo-arenosos, *Meyer 2074* (GH, LIL); en campos humedos, *Meyer 684* (LIL). ENRIQUE URIEN: *Meyer 4685* (LIL), *Schulz 3780* (LIL); Las Palmas, *Jorgensen 2316* (BA, GH, LIL, SI, US); Samuhi, *Escobar 13* (BAB, TAES); Chaco Central, *Asp 89* (SI); Laguna Blanca, *Aguilar 63* (LIL). CORRIENTES: Dpto. Monte Caseros: Libertad, costa arroya Curuzá, *Ibarrola 2511* (LIL); Goya, *Boelke 1519* (SI). ENTRE RIOS: Dpto. Feliciano: arroyo Puerto, *Castellanos 1170* (BA); Feliciano, *Crovetto & Cherini 6109* (BAB). Dpto. Concordia: Federal, *Molfino & Clos s.n.*, 31 Mar 1927 (BAB-p.p.), *L. H. s.n.*, 15 Feb 1917 (BA). Dpto. La Paz: Alcazar, *Krapovickas 7972* (LIL), *Saphis 239* (SI); Sauce de Luna, *Krapovickas 7971* (SI-p.p.); Algorrobenwald bei La Paz, *Lorentz 1428* (UC-p.p.); Gualeguaychú, *Jurado 15* (SI), *s.n.*, May 1920 (BA); Villaguay, Est. Santa Martha, *Müsch 36* (SI); Colonie Hernandarias, *Lorentz 1372* (UC); Colonia "Avigdor" Bovril FCE, *Krapovickas 261* (LIL). SANTA FE: Dpto. San Cristóbal: Arrufó, *Balegno 729* (LIL), "La Guasuncha" entre E. Rams y Hercitia, *Krapovickas 743* (LIL). Dpto. Gral. Obligado: Villa Ana, *Hayward 01464* (LIL), *01465* (LIL). Dpto. San Justo: La Criolla, *Castellanos 19560* (BA); 14 km S de Vera y Pintado, *Krapovickas & Cristóbal 14325* (CTES, TAES). Dpto. Vera: Caraquatay, borde de camino, isleta de sosque, *Krapovickas 7818* (LIL). Chaco Santafecino: Mocoví, *Venturi 190* (SI), *Lynch s.n.*, Nov 1903 (BA); Indio Muerto, *Comezaria 2727* (LIL); Videla, *Ragonese 2089* (BA-p.p.); Malabrigo FCSF, en el terraplén del FC, *Krapovickas 348* (LIL). CORDOBA: Dpto. Unión: Escuela de Bell-Ville, *s.n.*, 24 Apr 1907 (BAB). Dpto. San Justo: Balneario, *Balegno 1097* (LIL); Jeanmarie, en las inmediaciones de la Estación, *Hunziker 11367* (CORD, TAES); San Francisco, *Borsini 1254* (LIL). SANTIAGO DEL ESTERO: Dpto. Pellegrini: orilla del salitral, 500 m, *Venturi 5678* (GH, LIL, SI, US). TUCUMAN: Dpto. Leales: Chañar Poso, hab. terrenos salitrosos, 300 m, *Venturi 551* (BA, G, LIL, SI, US); *Diaz 63* (BAB). SALTA: *Lorentz & Hieronymus 1082* (GOET, UC). Dpto. Capital: Tiro Federal, *Correa 29* (LIL).

IN CULTIVATION: (provenance: Argentina) *Fryxell 15012* (TAES); (provenance: Texas) *Fryxell 15006* (ARIZ, TAES).

19. *Cienfuegosia* **integrifolia** (Chod. & Hassl.) Fryxell, comb et stat. nov.

C. sulphurea var. *integrifolia* Chod. & Hassl., Bull. Herb. Boiss. 2 ser., **5**: 302, 1905 [Type: in campis pr. Igatimi, Paraguay, 4 Nov 1898, *Hassler 5444* (Holotype: G-Herb. Boissier, isotypes: BM, G, NY, P)].

C. subprostrata var. *vera* Hassl., Repert. Spec. Nov. **7**: 379, 1909 (illegitimate, Article 63).

The same specimen is cited as type of both names cited above. Therefore, the name *C. subprostrata* var. *vera* Hassl. is nomenclaturally superfluous and must be rejected under Article 63.

Illustrations: none.

Low ascending herb arising from perennial rootstock. Stems glabrous, obscurely punctate, weakly angled. Leaves glaucous, minutely punctate, entire, 3(-5)-nerved, orbicular to obovate, truncate to cuneate, obtuse to apiculate. Petiole glabrate, canaliculate, obscurely punctate, 1-5 mm, rarely longer. Stipules narrowly linear, acuminate, often equaling or exceeding the petioles, 1-nerved, punctate, glabrate, persistent. Peduncles 3-10 cm (rarely to 18 cm) (exceeding leaves), glabrous, minutely punctate, incrassate above. Involucel of ca. 9 bractlets; bractlets often unequal, punctate, glabrous, 1-nerved, linear-lanceolate to weakly spatulate, ½ to 1½ cm long, 1-2 mm broad (adjacent bractlets sometimes connate forming broader element). Calyx, 12-18 mm, equaling or exceeding involucrum, obscurely punctate, glabrous to sparingly scabrous (on veins); lobes broadly

ovate, 5-8 mm broad, acute to acuminate, 3-5-nerved. Petals 3½ to 5 cm long, yellow with dark maroon spot having yellow radii. Androecium dark maroon throughout; anther mass obovate; anthers 5-ranked (?). Style greatly exceeding androecium (nearly equaling petals), punctate, reddish (?); stigma 3-lobed, dark red. Fruit (from immature example) ovoid, epunctate, rostrate, glabrous. Seeds unknown.

Distribution (Fig. 14): Paraguay: along the northeastern border in the Sierra de Maracayú and the Sierra de Amambai and southward as far as Caaguazú (at ca. 26° S. Lat.).

This species is known ecologically only from the few brief comments made by collectors: "in campis siccis," "campo colina," and "in campis combustis." The last comment suggests a similarity in its adaptation to that of *C. heteroclada* of Nigeria, a similarity that extends in part at least to its vegetative morphology.

PARAGUAY: In campis in regione vicine Igatimi, Sierra de Maracayú, *Hassler 5444* (BM, G, NY, P); prope Caaguazú, in campis siccis, *Hassler 9376* (G, K, NY, UC); Sierra de Amambay, in campis combustis Estrella, *Hassler 10221* (G); campo colina, *Rojas 6207* (G).

20. *Cienfuegosia subprostrata* Hochr., Ann. Cons. & Jard. Bot. Genève **6:** 57, 1902. [Type: In regione vicine San Estanislao, Sierra de Maracayú, Jan 1899, *Hassler 6011* (Holotype: G, isotypes: B (photo in MO), BM, GH, K, MO, NY, P, S, UC)].

Illustrations: Fig. 21, f-g.

Stems weak (trailing?), glabrous, ridged, obscurely punctate. Leaves entire, orbicular to ovate-elliptic, obtuse to acute, 5-nerved, obscurely punctate, reticulate, glabrous. Petioles canaliculate, punctate, ¼ length of lamina or longer (6-12 mm), glabrous or slightly hirsute near juncture with lamina. Stipules inconspicuous (1-2 mm), filiform, glabrate, caducous. Peduncle 2-4½ cm, costulate, obscurely punctate, glabrate to sparingly scabrous above. Involucel of 9-10 bractlets; bractlets lanceolate to spatulate, acute, 1-3-nerved, punctate, sparingly scabrous on margin and midrib (hairs 1 mm), 7-14 mm long, 1-3 mm broad. Calyx 12-17 mm (exceeding involucel), obscurely punctate, costulate, scabrous on veins and margin (hairs 1 mm); lobes 3-nerved, acute, ovate-lanceolate. Petals 3-4 cm, yellow with large maroon spot (with yellow radii). Androecium maroon throughout; anther mass obovate; anthers 5-ranked. Style greatly exceeding androecium (nearly equaling petals), punctate, whitish; stigma red, 3-lobed. Fruit 3-celled, ovoid, rostrate, 10-12 mm, ascending-sericeous. Seeds 4 mm, turbinate, comose; seeds hairs appressed, tan.

Distribution (Fig. 14): known only from central Paraguay in the vicinity of San Estanislao.

PARAGUAY: SAN PEDRO: In arenosis, in regione vicinis San Estanislao, Sierra de Maracayú, *Hassler 6011* (B, BM, G, GH, K, MO, NY, P. S, UC); Río Tapiracuay, 8 km de San Estanislao, camino a Rosario, campo cerca del río, *Krapovickas et al. 13945* (CTES, TAES).

7. SECT. **Friesia** Fryxell, sect. nov.

Herbae prostratae. Folia simplicia vel profunde dissecta. Stipulae auriculatae. Involucrum nullum. Petala epunctata. Capsulae glabrae intus.

Plants prostrate, herbaceous, arising from perennial woody rootstocks, glabrate to hirsute, punctate (but punctae very obscure). Leaves simple to lobed, parted or dissected, serrate or crenate. Stipules asymmetrical, auriculate-clasping (rarely falcate), acuminate. Flowers axillary, solitary, on unjointed peduncles; peduncles ascending in flower, recurved in fruit. Involucral nectaries lacking. Involucel lacking (although vestigial bractlets have been noted on individual specimens of two species). Calyx costulate, lobes acuminate or rarely acute. Petals epunctate, yellow, with or without dark spot on claw; spot when present sometimes having yellow radii. Style single or slightly divided apically. Stigmas capitate. Fruits 3-valved, glabrous within and without. Seeds appressed-hairy.

Type species: The type of sect. *Friesia* is *Cienfuegosia argentina* Gürke. The section is named in honor of R. E. Fries who, in describing *C. hispida* R. E. Fries, noted the alliance of this group of species.

Key to Species of Section Friesia

a. Leaves weakly lobed or variously parted; leaf margins crenate; tips of calyx lobes often hirsute.
  b. Leaves nearly simple to moderately parted (sometimes deeply and secondarily so), glabrate; style divided apically, stigmas light-colored ..... 21. *C. argentina*
  bb. Leaves weakly tri-lobed, hispid below and on petioles; style undivided; stigmas dark-red ..... 22. *C. hispida*
aa. Leaves simple or deeply dissected; leaf margins serrate; tips of calyx lobes glabrous.
  c. Leaves simple; stipules prominent (3-11 mm long, 2-6 mm broad); petioles ½ length of lamina or less ..... 23. *C. ulmifolia*
  cc. Leaves deeply dissected (or if simple, much reduced); stipules small (2-7 mm long, 1-3 mm broad); petioles ⅔ length of lamina or more..... 24. *C. hasslerana*

21. *Cienfuegosia argentina* Gürke in Mart., Fl. Bras. **12**(3): 579, 1892 [Type: Argentina: Salta: La Florida, Rio de Tala, Feb. 1873, *Lorentz & Hieronymus* 384 (Lectotype: UC; isolectotypes: MO (photo), BR, G, NY, US)].

Hibiscus argentinus Kuntze, Rev. Gen. Pl. 3(2): 19, 1898 non Speg. (1901).
Fugosia argentina Hochr., Ann. Cons. & Jard. Bot. Genève **4**: 172, 1900.

Gürke cites *Lorentz & Hieronymus s.n.* and *Lorentz & Hieronymus 1006*, in addition to the lectotype. These specimens therefore become paratypes.

Illustrations: Fig. 23, a-e; also Martius (1892) Pl. 113, fig. 2; Rodrigo (1948), Fig. 3 (labeled *C. argentina* var. *Hasslerana f. escholtzioides*); Fryxell (1963) Fig. 1, c & d (labeled *C. argentina* var. *hasslerana*); (1968) Fig. 3,l.

Stems procumbent, weakly ridged, very obscurely punctate (appearing epunctate), sometimes pubescent but more commonly glabrate. Leaves ovate, simple to variably divided, sometimes deeply digitately 3-5-divided, crenate, glabrate (sometimes minutely ciliate-margined, rarely hirsute), truncate, obtuse to acute, 5-nerved, punctate (but punctae detectable only on youngest leaves); lobes rounded, sometimes secondarily divided apically. Petioles canaliculate, ¼-½ (rarely to ¾) length of lamina, more or less pubescent near juncture with lamina, otherwise glabrate (rarely pubescent throughout), minutely punctate. Stipules sessile, auriculate (sometimes falcate), ciliate-margined (hairs ¾ mm), glabrous ventrally, pubescent to glabrate dorsally, 2-6 mm long, ⅓ mm broad, punctate, 1- (sometimes 3-)

nerved, persistent. Peduncles 1-6 cm, minutely puberulent (especially above) to glabrate, minutely punctate, slightly costulate. Involucel lacking. Calyx 15-ribbed, 10-18 mm, equaling or exceeding fruit, minutely pubescent throughout or glabrate (but usually pubescent apically), scarious intercostally, minutely and sparingly punctate (but punctae obscure and located close to veins: therefore often appearing epunctate); lobes 3-ribbed, ciliate-margined, generally pubescent at apex (hairs 1-1½ mm, ascending). Flowers sometimes cleistogamic. Petals with undulate margin, 2-3 cm, yellow with small dark-red spot on claw. Anther mass globose; filaments from pale to dark red; anthers yellow-orange. Style apically 3-parted, greenish, punctate, exceeding androecium; stigmatic lobes white to somewhat reddish in sicco, pubescent. Fruit epunctate (?), 3-loculed, 6-12 mm, ovoid. Seeds 3-4 mm, turbinate, comose; seed hairs appressed, brown, 3-5 mm. Embryo epunctate. Chromosome number: $n = 10$.

Distribution (Fig. 15): Argentina: abundant in the provinces of Tucumán and Salta, occurring in adjacent parts of Santiago del Estero and Catamarca, and extending as far southward as Córdoba. It extends northward into Bolivia and northeastward to central Paraguay.

Cienfuegosia argentina is a trailing herb that occurs primarily in open fields, apparently preferring sandy soils. Its principal distribution occurs at altitudes of 700-1500 m, but it probably also occurs at lower altitudes in Paraguay and at least as high as 1700 m in Bolivia.

BOLIVIA: Gran Chaco, Tatarenda, in campo aprico procumbens, *Fries 1446* (S); Quirusillas-Vallegrande, 1700 m, *Troll 929* (B, M).

PARAGUAY: Chaco Paraguayo, Isla Poi, *Rojas 7019a* (G); Carandayty, *Rojas 7179* (G).

Fig. 15. Distribution of *C. argentina* ● and *C. ulmifolia* ○. Fig. 16. Distribution of *C. hispida* ○ and *C. hasslerana* ●.

ARGENTINA: SALTA: Dpto. Anta: 1ª Sección, El Dorado, *Luna 1037* (LIL); 3ª Sección, *Luna s.n.*, 13 Feb 1948 (LIL); 10 km NE of Lumbreras, alt 710 m, *West 8396* (GH, MO, UC). Dpto. Candelaria: Ruiz de los Llanos, *O'Donell 4715* (LIL), *Schreiter 9439* (BA, LIL); en los campos, 1000 m, *R. S[chreiter] s.n.*, 26 Mar 1929 (LIL), *Venturi 8761* (GH, US); Quebrada Sta. Barbara, 1000 m, *Schreiter 5808* (F, LIL), *O'Donell 4718* (LIL); entre Ruiz de los Llanos y R. de la Frontera, *O'Donell 5460* (LIL). Dpto. Metán: camino de Horcones a El Porvenir, *Carenzo 322* (LIL); Lumbrera, *Ruiz 494* (LIL); Metán a Salta, *O'Donell 5482* (LIL); entre Metán y R. de los Llanos, *Legname & Cuezzo 3035* (LIL). Rosario de la Frontera: *Schreiter 1549* (B, BAB, F, LIL, TAES, US), *Lillo 4402* (F, G-3 sheets, one of which is labelled "Trancas, Prov. Tucuman," LIL, NY), *de la Sota 86* (LIL). Río de Tala: La Florida, *Lorentz & Hieronymus 384* (B, BR, G, MO - as photo, NY - labelled "prov. Catamarca" rather than "prov. Salta," UC, US); cerca de La Cañada, *2540* (LIL), *Meyer 21185* (LIL); Cormel Moldes, a orilla del Río Chanapampa, *Hunziker 1159* (LIL, NY); camino de Salta a Tucumán, *Villalón s.n.* (LIL); Joaquim V. Gonzales, *Aguilar 269* (LIL); Güemes, *Meyer 8368* (LIL). TUCUMAN: Dpto. Trancas: Río Tala, *Venturi 7370* (US), *Rodriguez 12* (G, LIL, US); zwischen Alduralde und Trancas, *Lorentz & Hieronymus 1006* (UC); a San Pedro de Colalao, *Schreiter 7414* (LIL); Burrucayu, *Stuckert 12821* (G), *9128* (G), *16969* (G, LIL, S), *Wall 37* (S), *Diaz 3* (BAB, TAES). CORDOBA: Los Mogotes, Sierra Chica de Córdoba, *Holmberg s.n.*, 6 Feb 1877 (BA). CATAMARCA: Dpto. Ancasti: Las Tunas, *Spegazzini s.n.*, 14 Feb 1910 (BAB), *s.n.*, 20 Feb 1910 (BAB). SANTIAGO DEL ESTERO: Dpto. Robles: Furena, *Maldonado 241* (NY, S), *Argañarás 144* (SI); Garza, *Krapovickas 10043* (LIL); entre Beltán y El Simbolar, *Krapovickas 10042* (LIL); El Simbolar, *Krapovickas 10041* (LIL).

IN CULTIVATION: (provenance: Colonia Benitez, Chaco, Argentina) *Fryxell 15003* (ARIZ, LE, TAES).

22. *Cienfuegosia hispida* R. E. Fries, Kungl. Sv. Vet. Handl. **24:** 33, 1947 [Type: Argentina: Salta: orilla de un salitral, Cerro Negro, Antillas, 700 m, 19 Mar 1930, *Venturi 10311* (Holotype: S, isotypes: GH, MO, NY, US)].

Illustrations: Fig. 23, f-h; also Fries (op. cit.) Pl. 7, fig. 2; Rodrigo (1948) Fig. 1, A-E.

Stems procumbent, hirsute (hairs 1 mm) becoming glabrate, apparently epunctate. Leaves ovate to weakly 3-lobed, dentate, truncate, obtuse to acute, sparingly hirsute becoming glabrate above, hispid below (primarily on veins), ciliate-margined, nearly as broad as long, 3-5-nerved. Petioles densely hispid throughout, canaliculate, punctate, ¼-⅓ (rarely ½) length of lamina. Stipules subulate to auriculate, sessile, hirsute (on vein) to glabrate, ciliate-margined, 3-4 mm long, 1-3 mm broad (sometimes larger), persistent. Peduncles 2-2½ cm (sometimes longer), sparsely hispid, obscurely punctate. Involucel lacking (one vestigial bractlet is discernible on the holotype). Calyx 15-ribbed, 12-20 mm, densely hispid in bud, moderately so in flower and fruit (especially on veins and margin), apparently epunctate; lobes lanceolate, acuminate, 3-ribbed. Petals 2-3 cm, yellow with large dark-red spot. Androecium dark red; anthers orange (?). Style exceeding androecium, whitish; stigma red, pubescent. Fruit 8-10 mm, glabrous (?). Seeds comose; seed hairs tan.

Although *C. hispida* is closely allied to the other species of sect. *Friesia* and is known only from a relatively few specimens, it appears to be a distinct taxon, distinguished by its vestiture, its large seeds (according to Rodrigo, 1948), its large petal spot, and its leaf form.

Distribution (Fig. 16): Argentina: provinces of Salta, Tucumán, and Santiago del Estero. In addition Rodrigo (1948) cites and illustrates a specimen (*Berti &*

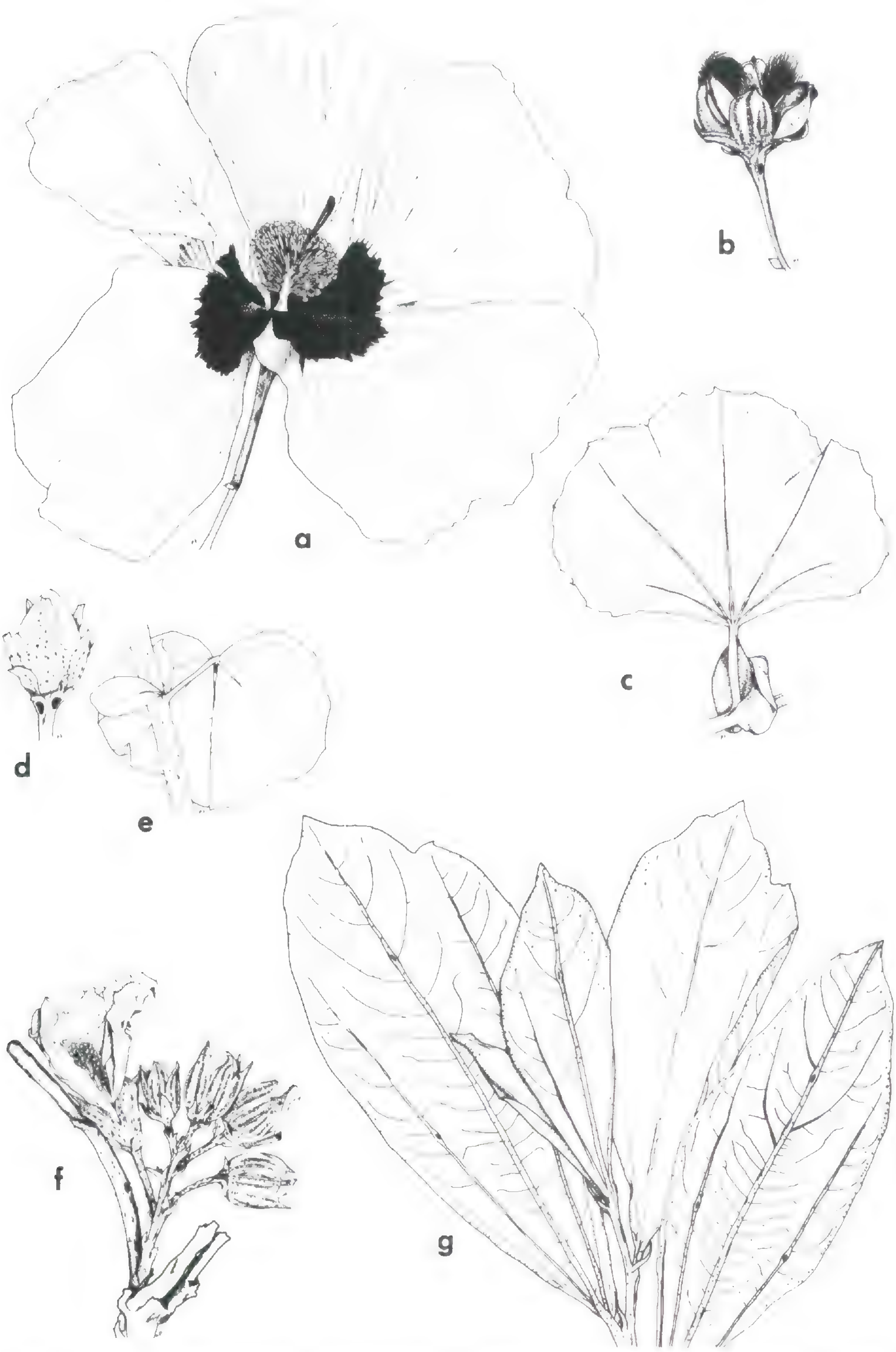


Fig. 17. A-C, *Cienfuegosia hildebrandtii* Garcke: A, flower [*Fryxell 14007* (TAES)]; B, mature fruit [*Fryxell 14001* (TAES)]; C, leaf [*Fryxell 14007* (TAES)]. D-E, *Cienfuegosia gerrardii* (Harv. ex Harv. & Sond.) Hochr.: D, bud [*Liebenberg 3492* (PRE)]; E, leaf [*Wood 11722* (PRE)]. F-G, *Cienfuegosia heteroclada* Sprague: F, tip of vegetative shoot [*Ahiekpor s.n.* (GC)]; G, flowering shoot, arising from base of preceding year's stem [*Enti & Agyakwa s.n.* (GC)]. All × 1.

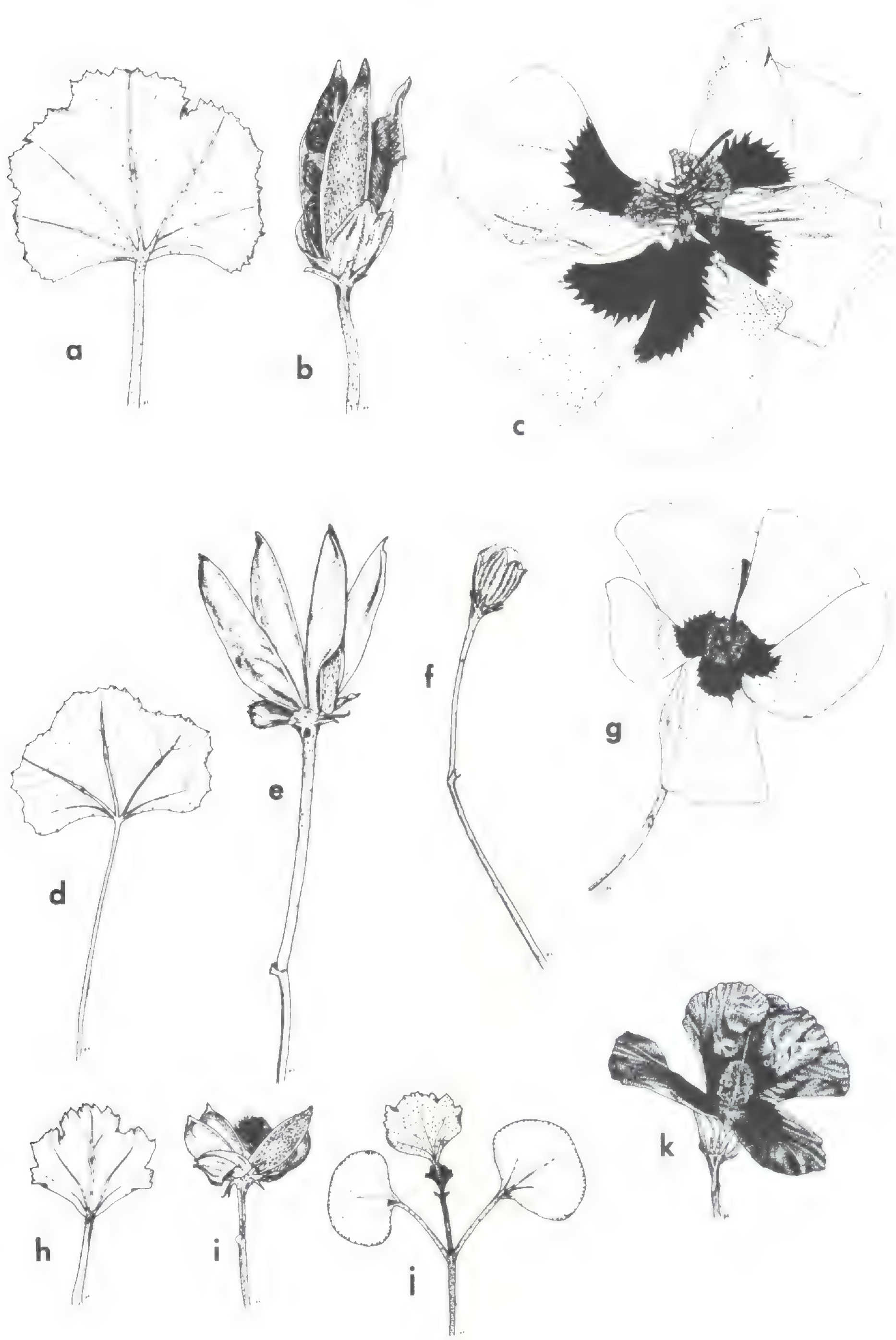


Fig. 18. A-C, *Cienfuegosia somaliana* Fryx. [*Fryxell s.n.* (TAES)]: A, leaf; B, mature fruit; C, flower. D-G, *Cienfuegosia welshii* (Anders.) Garcke [*Fryxell 14006* (TAES)]: D, leaf; E, mature fruit; F, bud; G, flower. H-K, *Cienfuegosia hearnii* Fryx. [*Fryxell 14005* (TAES)]: H, leaf; I, mature fruit; J, seedling with cotyledons shown; K, flower. All × 1.

Escalante 417, LP -n.v.) from Corrientes. The type is from a saline environment.

ARGENTINA: SALTA: Antillas, Cerro Negro 700 m, orilla de un salitral, *Venturi 10311* (GH, MO, NY, S, US). TUCUMAN: Dpto. Leales, La Florida, hab. bosque, 300 m, *Monetti 14711* (G, LIL). SANTIAGO DEL ESTERO: Dpto. Leales, Los Puestos, *Meyer 12798* (LIL).

23. *Cienfuegosia ulmifolia* Fryx., Britt. **19:** 35, 1967 [Type: Argentina: Chaco: Colonia Benitez, Dec. 1928, *Schulz 170* (Holotype: BAB)]

Illustrations: Fig. 23, i-k; also Rodrigo (1941) Fig. 1, Fig. 3A (both labelled *C. argentina*); Fryxell (1967a) Fig. 1, a-d.

Stems weakly ridged, obscurely and minutely punctate (sometimes apparently epunctate), sparingly pubescent to glabrate, reddish-brown. Leaves simple, ovate to elliptic, serrate, truncate, acute, glabrate (or sparingly hirsute below), sometimes sparingly ciliate, 5-veined; veins reddish-brown below. Petioles ¼-½ length of lamina, obscurely punctate, glabrate or sparingly puberulent near juncture with lamina, canaliculate, reddish-brown. Stipules sessile, auriculate (rarely falcate), acuminate (rarely toothed), glabrate or weakly ciliate, persistent, 3-11 mm long, 2-6 mm broad, 1-nerved, sometimes exceeding petioles. Peduncles 1-6 cm, weakly ridged, sparsely pubescent to glabrate, obscurely punctate. Involucel lacking. Calyx 15-ribbed, 10-20 mm (exceeding fruit), obscurely punctate, glabrous (or sometimes with a few scabrous hairs toward base of calyx tube, but none on apices of calyx lobes); calyx lobes 3-ribbed, lanceolate, acuminate to acute, glabrous. Petals 2-4 cm, yellow with large maroon spot on claw having yellow radii. Androecium maroon throughout; anther mass obovoid. Style sparsely punctate, exceeding androecium, undivided (or sometimes divided apically in sicco); stigma dark-red, pubescent, 3-lobed. Fruit 3-loculed, epunctate, 8-10 mm, globose to ovoid. Seeds 4-5 mm long, hairy; hairs appressed, tan. Embryo epunctate. Chromosome number: $n = 10$.

Distribution (Fig. 15): Paraguay: in the valley of the Río Paraguay from its confluence with the Río Apa south to the confluence with the Río Paraná; Argentina: Chaco, Corrientes, and Santa Fé in the valley of the Río Paraná. A single specimen from Tucumán extends this distribution to the west. This species occurs on sandy soils, on heavy clay, and frequently in saline situations.

PARAGUAY: BOQUERON: Puerto Casado, Estancia "Maria Casilda," *Pedersen 4099* (BR, C, G, GH, US), *Gregory et al. 10604* (LIL); Chaco Paraguayo, Orihuela, campo palmas, *Rojas 5208* (G); Isla Poi-Orihuela, campo tierra arenosa, *Rojas 7019* (G); San Salvador, dans les argiles impermeables, *Balansa 1875a* (P-p.p.); Itapucumí, *Rojas 2599* (G, M).

ARGENTINA: CHACO: Dpto. Resistencia, Colonia Benitez, *Schulz 170* (BAB), *622* (S), *10998* (LIL); Fontana, *Meyer 2075* (GH, LIL). CORRIENTES: Dpto. Mburucuyá: Estancia Santa Teresa, *Pedersen 477* (BR, C, P, S, US), *Schwarz 8700* (LIL); Empedrado, *Schwarz 9949* (LIL-p.p.). Dpto. San Luis del Palmar: 25 km E de S. Luis del Palmar, *Krapovickas & Cristóbal 11805* (TAES). SANTA FE: Mocoví, Ocampo, *Venturi 190* (BA, BAB, LIL, TAES), *Venturi 190 bis* (SI); Videla, *Ragonese* (BA-p.p.); Malabrigo, *Castellanos 19563* (BA). TUCUMAN: *Diaz 56* (BAB).

24. *Cienfuegosia hasslerana* Hochr. ex Chod. & Hassl., Bull. Herb. Boiss., ser. 2, **5**: 302, 1905 [Type: Paraguay: in arenosis salsis in regione cursus superioris fluminis Apa, Oct 1901, *Hassler 7686* (Lectotype: G, isotypes: B (as photo MO), BM, GH, MICH, NY, P, S, UC)].

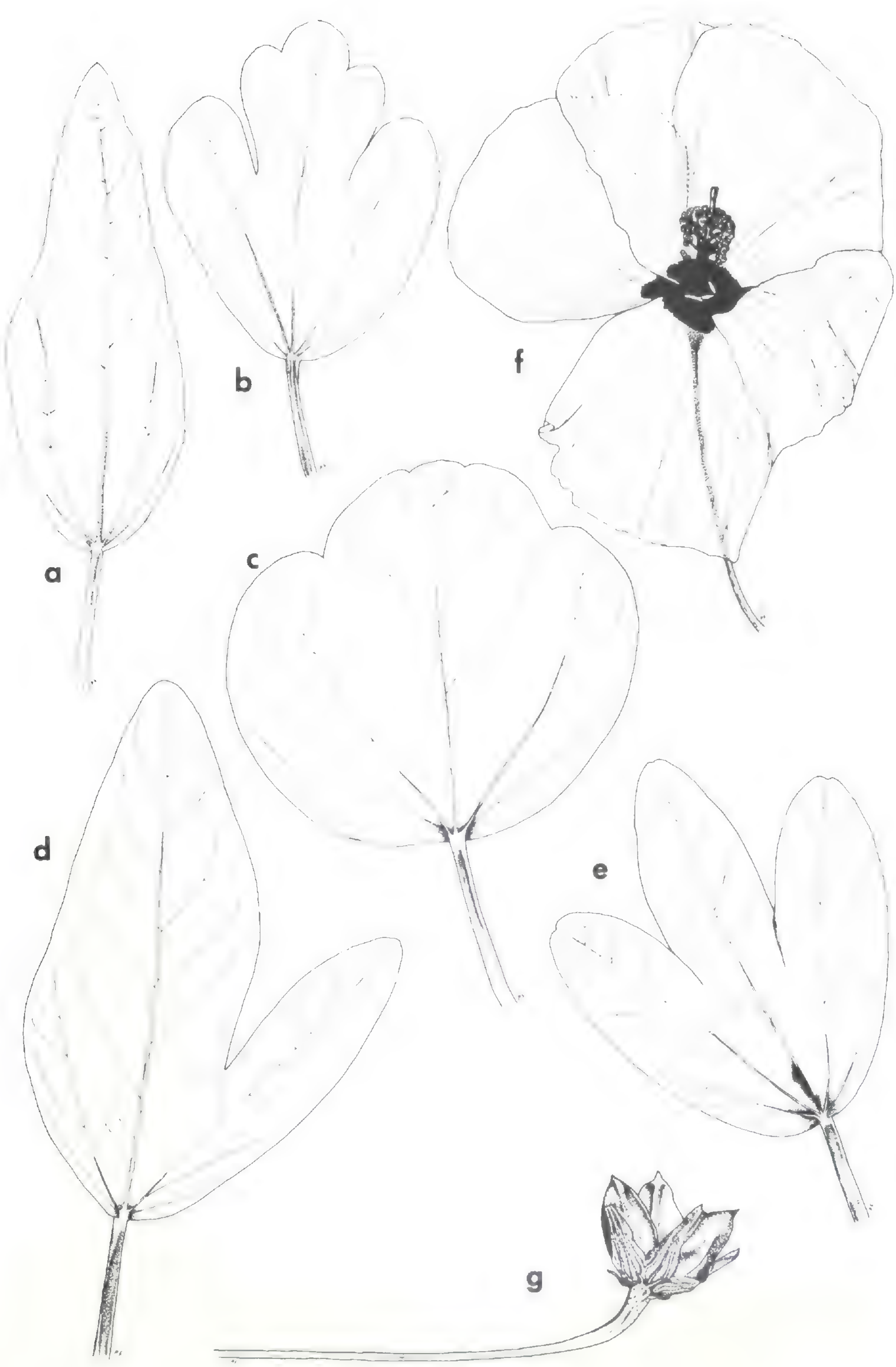
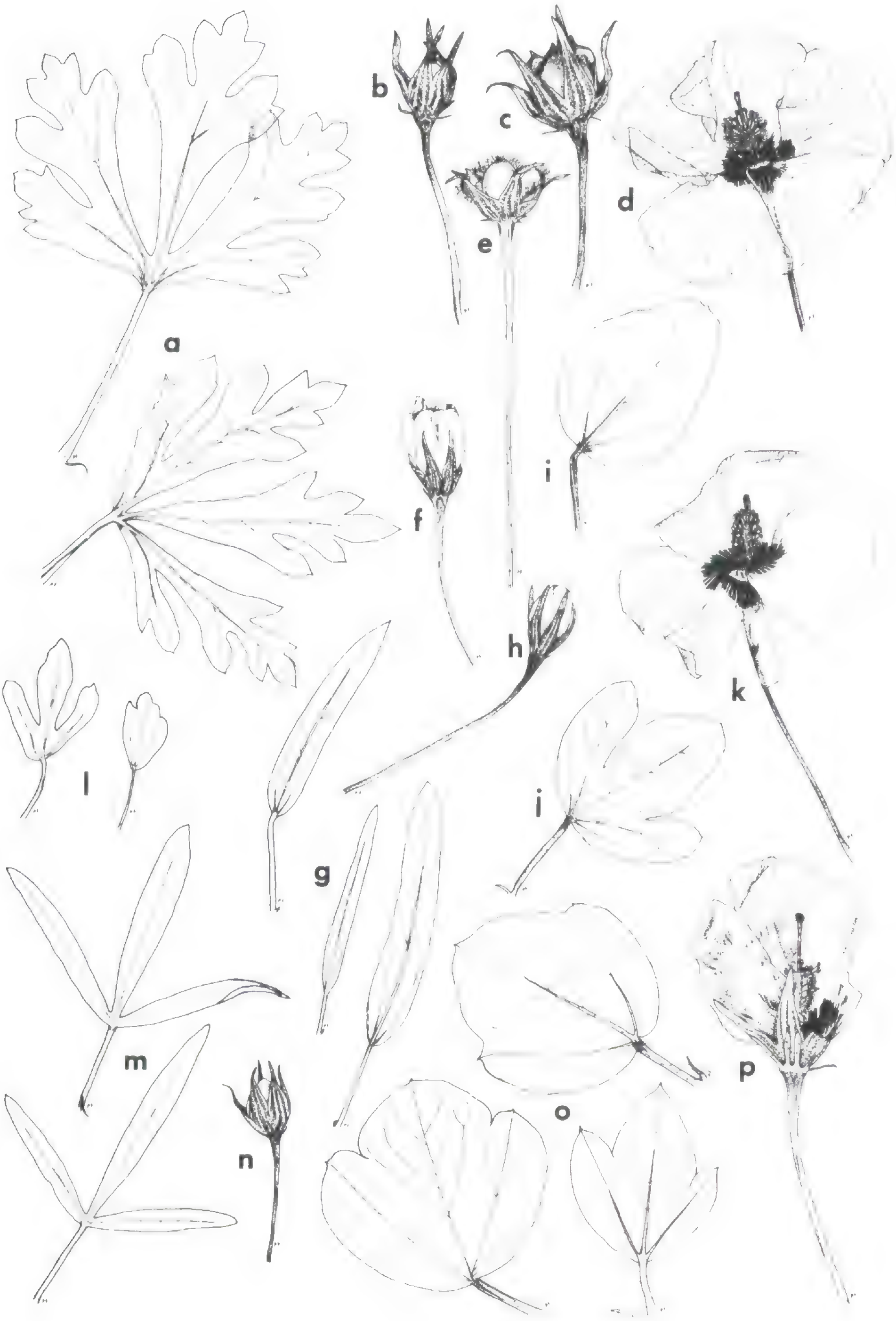


Fig. 19. *Cienfuegosia tripartita* (H.B.K.) Gürke [*Fryxell s.n.* (TAES)]: A-E, leaves, showing some of the variability encountered; F, flower; G, mature fruit. All × 1.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C. argentina var. *hasslerana* Hassl., Repert. Spec. Nov. **7**: 381, 1909.
C. escholtzioides Hochr. ex Chod. & Hassl., Bull. Herb. Boiss., ser. 2, **5**: 302, 1905 [Type: Paraguay: in arenosis salsis in regione cursus superioris fluminis Apa, Nov 1901, *Hassler 7686a* (Lectotype: G, isotypes: BM, NY, S, UC)].
C. argentina var. *hasslerana* f. *escholtzioides* Hassl., Repert. Spec. Nov. **7**: 381, 1909.

None of the duplicates of *Hassler 7686* can be definitely identified as the holotype of *C. hasslerana*. Only the Geneva and British Museum specimens bear the name *C. hasslerana* Hochr., and in both cases the handwriting is Hassler's rather than Hochreutiner's. Unless the holotype is subsequently discovered, the specimen kept at Geneva is here designated as lectotype. The problem of identifying the holotype of *C. escholtzioides* is similar, and the Geneva specimen of *Hassler 7686a* is also designated as lectotype:

Illustrations: Fig. 23, l-o.

Stems slender, weakly ridged, obscurely punctate, glabrate. Leaves glabrate, pinnatisect to moderately parted (or sometimes simple, cuneiform, and apically dentate on reduced lower leaves). Petiole canaliculate, glabrous or slightly hirsute near juncture with lamina, ⅔ length of to equaling lamina, obscurely punctate. Stipules auriculate (sometimes subulate), sessile, glabrous to ciliate, 1-nerved, minutely punctate, 2-7 mm long, 1-3 mm broad. Peduncles glabrate (or with a few bristles at summit), obscurely punctate, 2-4½ cm, ridged. Involucel lacking (vestigial bractlets discernible on *Balansa 1875a* and *Krapovickas et al. 14249*). Calyx 10-18 mm, 15-ribbed, glabrate or somewhat bristly basally but glabrous apically, scarious intercostally, obscurely punctate (sometimes appearing epunctate); lobes 3-ribbed, glabrous, narrowly lanceolate, acuminate, sometimes acute). Petals 2-3½ cm, yellow with large maroon spot having poorly developed yellow radii on claw. Androecium maroon throughout; anther mass obovoid. Style greatly exceeding androecium (nearly equaling petals), punctate, pallid, undivided (or sometimes slightly divided); stigma pubescent, pink to red, 3-lobed. Fruit epunctate, elliptic, 8-10 mm, 3-loculed. Seeds 3-4 mm, comose; seed hairs appressed, tan.

The leaf of *C. hasslerana* is characteristically deeply dissected, but plants produce occasional reduced, undissected leaves. This variability reaches its extreme expression in an isotype of *C. hasslerana* (*Hassler 7686*, UC). Other sheets of this same plant, notably the lectotype (G), show the deeply dissected leaf typical of the species. Both types of leaves are found on the same branch in many specimens, such as another isotype (S).

Distribution (Fig. 16): Paraguay and southward into the Argentine province of Corrienties.

Fig. 20. A-D, *Cienfuegosia digitata* Cav. [*Fryxell 14008* (TAES)]: A, two leaves; B, bud; C, mature fruit; D, flower. E G, *Cienfuegosia yucatanensis* Millsp.: E, mature fruit [*Fryxell s.n.* (TAES)]; F, day-old flower [*Dunbar 146* (GH)]; G, three leaves [*Dunbar 146* (GH)]. H-K, *Cienfuegosia heterophylla* (Vent.) Garcke [*Miller & Johnston 66* (GH)]: H, bud; I-J, leaves; K, flower. L-N, *Cienfuegosia subternata* (Hassl.) Fryx. [*Fiebrig 4022* (GH)]: L, two reduced lower leaves; M, two climax leaves; N, bud. O-P, *Cienfuegosia rosei* Fryx. [*Nelson 2779* (GH)]: O, three leaves; P, flower. All × 1.

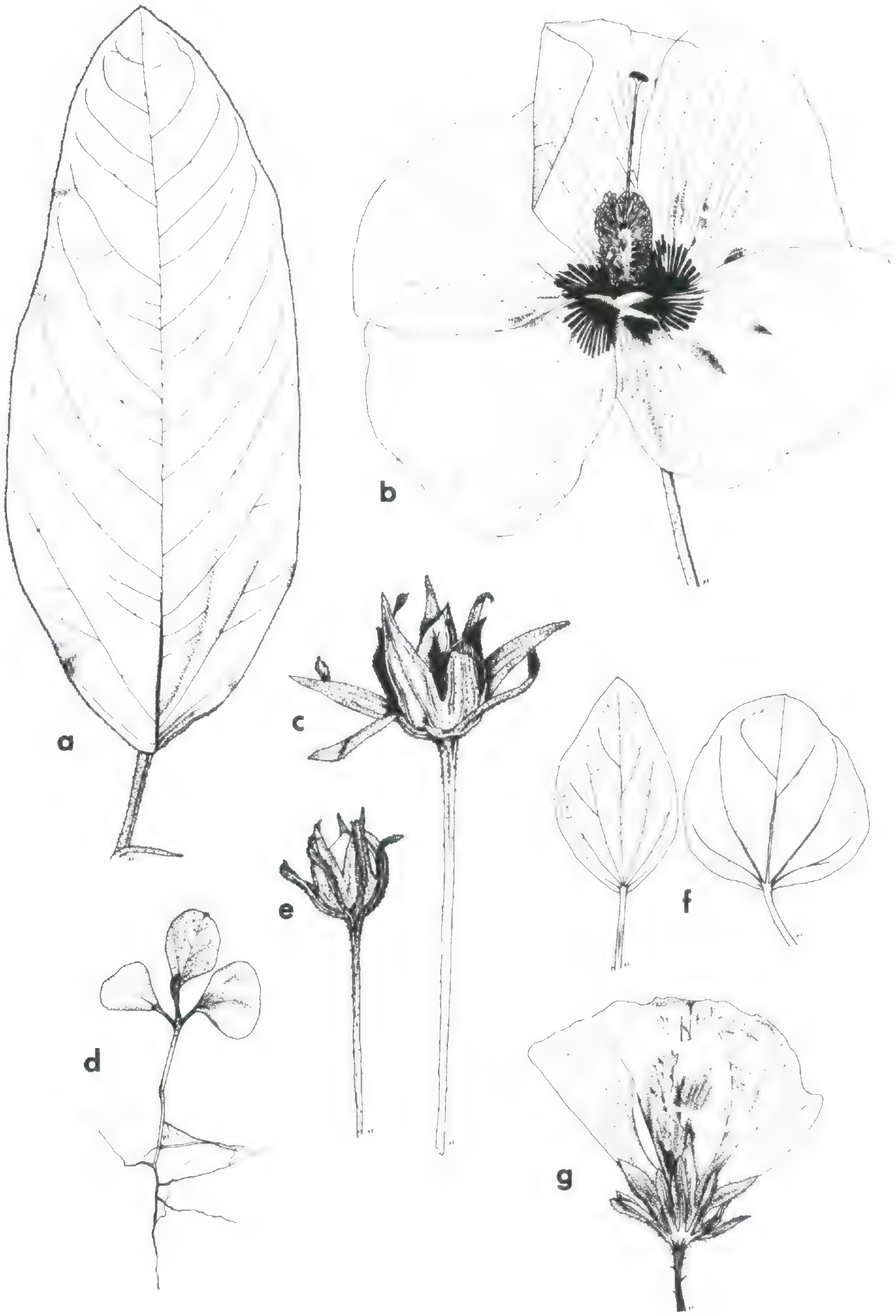

Fig. 21. A-E, *Cienfuegosia affinis* (H.B.K.) Hochr. [*Fryxell 15011* (TAES)]: A, leaf; B, flower; C, mature fruit; D, seedling with cotyledons shown; E, bud. F-G, *Cienfuegosia subprostrata* Hochr. [*Hassler 6011* (GH)]: F, two leaves; G, flower. All × 1.

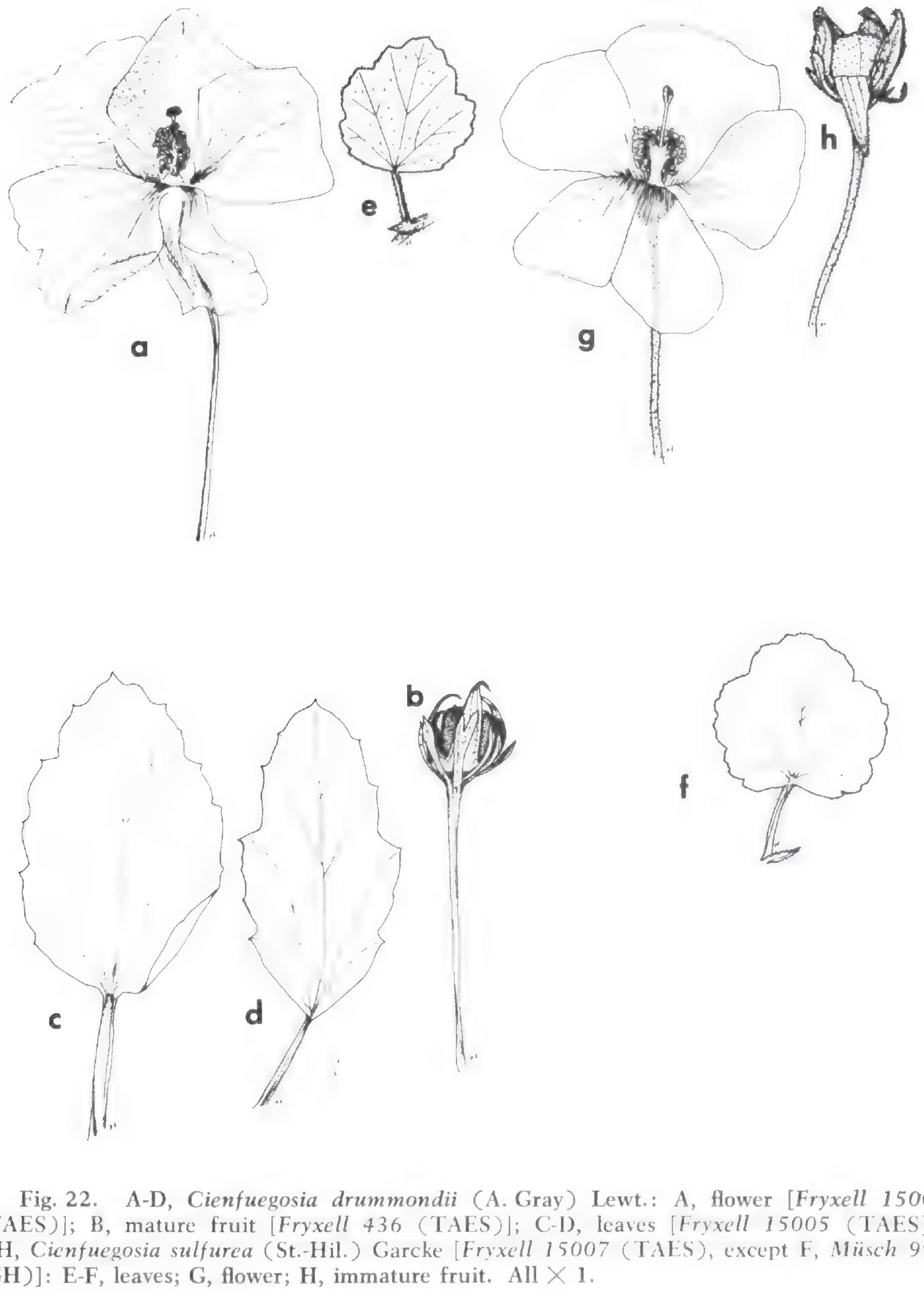

Fig. 22. A-D, *Cienfuegosia drummondii* (A. Gray) Lewt.: A, flower [*Fryxell 15005* (TAES)]; B, mature fruit [*Fryxell 436* (TAES)]; C-D, leaves [*Fryxell 15005* (TAES)]. E-H, *Cienfuegosia sulfurea* (St.-Hil.) Garcke [*Fryxell 15007* (TAES), except F, *Müsch 995* (GH)]: E-F, leaves; G, flower; H, immature fruit. All × 1.

The ecological adaptation of this species is apparently similar to that of the other species of this section. A notation on the type, "in arenosis salsis," indicates an affinity for sandy soils and a saline environment.

PARAGUAY: In arenosis salsis in regione cursus superioris fluminis Apa, *Hassler 7686* (B, BM, G, GH, MICH, MO, NY, P, S, UC), *7686a* (BM, G, NY, S, UC); zwischen Río Apa und Río Aquidabán, *Fiebrig 5000* (G, K, L); alto Paraguay, San Salvador, *Rojas 2587*

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(G, M), *Balansa 1875a* (P-p.p.); Belén (20 km SE de Concepción) en campo, *Krapovickas et al. 14249* (CTES, TAES).

ARGENTINA: CORRIENTES: Arroyo Mocoretá, *Castellanos 34435* (BA, M); Dpto. Mburucuyá, Santa Maria, *Pedersen 5042* (C, P, S); Paso de los Libres, 10 km al NW, *Cristóbal et al. 86* (LIL).

REJECTED NAMES AND EXCLUDED SPECIES

Rejected names:

Cienfuegosia affinis var. *humilis* (Gürke) Hochr. — illegitimate, Article 63.
C. Benthamii Hochr. — illegitimate, Article 67.
C. Drummondii var. *genuina* Hassl. — illegitimate, Article 26.
C. phlomidifolia var. *humilis* Gürke — illegitimate, Article 63.
C. punctata (Cunn. ex Benth.) Domin — illegitimate Articles 64 and 67.
C. subprostrata var. *vera* Hassl. — illegitimate, Article 63.
C. sulphurea (H.B.K.) Hassl. — illegitimate, Article 64.
All combinations with *Fugosia* Juss. must also be rejected, as discussed on p. 180, because of the priority of *Cienfuegosia* Cav.

Excluded species (including combinations both in *Cienfuegosia* and in *Fugosia*):

C. althaeoides Chiov.	(= *Hibiscus ludwigii* Eckl. & Zeyh.)
C. anomalum (Wawr.) Gürke	(= *Gossypium anomalum* Wawr. ex Wawr. & Peyr.)
C. australis (F. Muell.) K. Schum. = *F. australis* (F. Muell.) Benth.	(= *Gossypium australe* F. Muell.)
C. australis var. *microcarpa* Domin.	(= *Gossypium australe* F. Muell.?)
C. Benthamii Hochr. [basionym: *F. punctata* Cunn. ex Benth.]	(= *Gossypium cunninghamii* Tod.)
C. Bricchetti Ulbr.	(= *Gossypium somalense* (Gürke) Hutch.)
C. cuneiformis (DC.) Hochr. = *F. cuneiformis* (DC.) Benth.	(= *Alyogyne cuneiformis* (DC.) Alef.)
C. Ellenbeckii Gürke	(= *Gossypium somalense* (Gürke) Hutch.)
C. flaviflora (F. Muell.) Hochr. = *F. flaviflora* F. Muell.	(= *Thespesia lampas* (Cav.) Dalz. ex Dalz. & Gibs. var. *thespesioides* (*R. Br. ex* Benth.) Fryx.)
C. gossypioides (R. Br.) Hochr.	(= *Gossypium sturtianum* J. H. Willis)
C. hakeaefolia (Giord.) Hochr. = *F. hakeaefolia* (Giord.) Hook.	(= *Alyogyne hakeaefolia* (Giord.) Alef.)
C. hakeaefolia var. *lilacina* (Lindl.) Hochr. = *F. lilacinus* (Lindl.) G. Don ex Loud.	(= *Alyogyne hakeaefolia* (Giord.) Alef.)
C. incana Schwartz	(= *Gossypium incanum* (Schwartz) Hillc.)
C. latifolia (Benth.) Hochr. = *F. latifolia* Benth.	(= *Gossypium costulatum* Tod.)
C. Palmeri Rose	(= *Gossypium aridum* (Rose & Standl.) Skov.)
C. pedata (Bail.) Domin. = *F. pedata* Bail.	(= *Gossypium bickii* Prokh.)
C. pentaphylla K. Schum.	(= *Gossypium anomalum* Wawr. ex Wawr. & Peyr.)

Fig. 23. A-E, *Cienfuegosia argentina* Gürke [*Fryxell 15003* (TAES)]: A, seedling with cotyledons shown; B, immature fruit; C, mature fruit; D, flower; E, leaf. F-H, *Cienfuegosia hispida* R. E. Fries [*Venturi 10311* (GH)]: F, flower; G, three leaves; H, mature fruit. I-K, *Cienfuegosia ulmifolia* Fryx.: I, leaf [*Krapovickas & Cristóbal 11805* (TAES)]; J, immature fruit [*Pedersen 4099* (GH)]; K, flower [*Krapovickas & Cristóbal 11805* (TAES)]. L-O, *Cienfuegosia hasslerana* Hochr. ex Chod. & Hassl. [*Hassler 7686* (GH)]: L, two climax leaves; M, two reduced, lower leaves; N, flower; O, immature fruit. All × 1.

C. populifolia (Benth.) Hochr. = *F. populifolia* Benth.	(= *Gossypium populifolium* (Benth.) F. Muell. ex Tod.)
C. pulchella C. A. Gardn. = *F. pulchella* C. A. Gardn.	(= *Gossypium pulchellum* (C. A. Gardn.) Fryx.)
C. punctata (Cunn. ex Benth.) Domin. = *F. punctata* Cunn. ex Benth.	(= *Gossypium cunninghamii* Tod.)
C. robinsonii (F. Muell.) Hochr. = *F. robinsonii* F. Muell.	(= *Gossypium robinsonii* F. Muell.)
C. somalensis Gürke	(= *Gossypium somalense* (Gürke) Hutch.)
C. thespesioides (R. Br. ex Benth.) Hochr. = *F. thespesioides* R. Br. ex Benth.	(= *Thespesia lampas* (Cav.) Dalz. ex Calz & Gibs. var. *thespesioides* (R. Br. ex Benth.) Fryx.)
C. triphylla (Harv. ex Harv. & Sond.) K. Schum. = *F. triphylla* Harv. ex Harv. & Sond.	(= *Gossypium triphyllum* (Harv. ex Harv. & Sond.) Hochr.)
F. areysiana Deflers	(= *Gossypium areysianum* Deflers)
F. Grantii (Mast. ex Oliv.) Hochr.	(= *Kosteletzkya Grantii* (Mast. ex Oliv.) Garcke)
F. hakeaefolia var. *coronopifolia* (Miq.) Benth.	(= *Alyogyne hakeaefolia* (Giord.) Alef.)

In addition to the preceding rejections and exclusions, a few additional names have appeared in the literature that have apparently never been validly published. These names have no standing under the Rules and must be regarded as *nomina nudae*. They are:

C. Dinteri Ulbr. ex Skov nom. nud.	(= *Gossypium herbaceum* var. *dinteri* Ulbr.?)
F. hildebrandti ex Youngman	
C. cuneata (Benth.) Hutch. nom. nud.	
F. sulphurea var. *trifida* Griseb. ex Rodrigo nom. nud.	

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Index of Collectors

(Type specimens in boldface)

Adams 4013
——— & Akpabla 4364
Adanson **145A**
Aguilar 269
— — — 640, 1037
——— 63, 1263
——— 1171

Ahiekpor s.n.
Andersson 135
Ansits 2163
Arechavaleta **1524**
Argañarás 144
Asp 89
Asplund 5661
Baez 12
——— 75
Balansa 1875
— — 1875*a*

Balegno 612
——— 729, 1097
Bally 9674, 11910
Basaldua s.n.
Bebbington 1693
Beccari s.n.
Berhaut 1344
Berro 1466
Berti & Escalante 417
Blanchet **2702**
Blaumer 9
Blodgett s.n.
Boelcke 1519
Boldingh 6383
Borle 257, 551
Borsini 1254
Brade 13440
Braga 82
Breyer 20592
Britton 521
——— & Britton 211
Buckley s.n.
Buratovich 284, 338
Burchell 5620
Burtt-Davy 10572
Buswell 1387

C. heteroclada
C. heteroclada
C. digitata
C. argentina
C. sulfurea
C. drummondii
C. sulfurea &
C. drummondii
(mixed)
C. heteroclada
C. tripartita
C. drummondii
C. sulfurea
C. argentina
C. drummondii
C. tripartita
C. drummondii
C. sulfurea
C. drummondii
C. ulmifolia &
C. hasslerana
(mixed)
C. sulfurea
C. drummondii
C. somaliana
C. drummondii
C. digitata
C. welshii
C. digitata
C. sulfurea
C. hispida
C. heterophylla
C. heterophylla
C. yucatanensis
C. drummondii
C. heterophylla
C. hildebrandtii
C. drummondii
C. affinis
C. hildebrandtii
C. digitata
C. heterophylla
C. heterophylla
C. drummondii
C. drummondii
C. affinis
C. hildebrandtii
C. yucatanensis

Cabrera 10572
Carenzo 322
Castellanos 34435
——— s.n., 1168, 34437
——— 19563
——— 1170, 19560
Chapman s.n.
——— 3041
Chevalier s.n., 24535
Claussen 374, 549, 590
Clover 1259
Codd 5229
— — — 8873
Comezaria 2727
Correa 29
Cristóbal, Ahumada & de
la Sota 86
Crovetto & Cherini 6109
——— & Leguizamon
4913
——— & Piccinini 4701
Curran & Haman 1072
Curtiss 398
DaCosta 27A
Dagueri 967
Dalziel **122**
Davey 224, 233
DeCarvalho 219
Deflers s.n., 60
Dennis 2278
DeWinter & Leistner 5110
Diaz 3
——— 56
——— 63
Dinter **669**, 7215, 7459
Drummond, T. **42**
Drummond, R. B. &
Hemsley **2285**
——— & Seagrief 5215
Drushell 114, 176
Ducke 2068
Dunbar 146
Dupré s.n.
Edwards 3298
Eggers 350
——— 13560
——— 14767
Eifrig 21

C. sulfurea
C. argentina
C. hasslerana
C. sulfurea
C. ulmifolia
C. drummondii
C. yucatanensis
C. drummondii
C. digitata
C. affinis
C. drummondii
C. hildebrandtii
C. digitata
C. drummondii
C. drummondii

C. hasslerana
C. drummondii

C. sulfurea
C. sulfurea
C. affinis
C. yucatanensis
C. affinis
C. drummondii
C. heteroclada
C. digitata
C. hildebrandtii
C. welshii
C. affinis
C. digitata
C. argentina
C. ulmifolia
C. drummondii
C. digitata
C. drummondii

C. hildebrandtii
C. digitata
C. drummondii
C. affinis
C. yucatanensis
C. sulfurea
C. hildebrandtii
C. heterophylla
C. affinis
C. tripartita
C. drummondii

Ekman 15487 C. yucatanensis
Elias 183, 223, 398 C. affinis
Enti & Agyakwa s.n. C. heteroclada
Escobar 13 C. drummondii
Exell & Mendonça 2694, 2789, 2872 C. digitata
Fendler 105, 106 C. affinis
Ferreyra 5962 C. tripartita
Fiebrig 1233 C. drummondii
——— 4022, 5230 C. subternata
——— 5000 C. hasslerana
Flossdorf s.n. C. drummondii
Fries 1446 C. argentina
Fruchard s.n. C. sulfurea
Fryxell s.n. C. somaliana
——— s.n. C. tripartita
——— 436, 701, 15006, 15012 C. drummondii
——— 749 C. rosei
——— 14001, 14007 C. hildebrandtii
——— **14005** C. hearnii
——— 14006 C. welshii
——— 14008 C. digitata
——— 15003 C. argentina
——— 15004, 15010 C. heterophylla
——— 15007 C. sulfurea
——— 15011, 15016 C. affinis
——— s.n., 15013 C. yucatanensis
——— & Bates 906 C. rosei
Funck 181 C. affinis
——— & Schlim **700** C. affinis
Galpin 12193 C. gerrardii
Garber s.n. C. yucatanensis
Garcia s.n. C. sulfurea
Gardner 1459 C. affinis
——— 2399 C. heterophylla
Gaudichaud 44 C. affinis
Gaumer 1269 C. yucatanensis
Gerrard 257, **632** C. gerrardii
——— & McKen. s.n. C. gerrardii
Gillett 4239 C. somaliana
Glaziou 18882, 20714 C. affinis
Glover & Gilliland **1206**, 1216 C. somaliana
Gooding 207 C. welshii
Graham 248 C. affinis
Gregory, Krapovickas & Pietrarelli 10601 C. drummondii
——— 10604 C. ulmifolia
——— 9908 C. affinis
Grosourdy s.n. C. affinis
Guichard 122, 122A C. hearnii
Hagerup 385*a* C. digitata
Hanson s.n. C. drummondii
Harbor 6481 C. digitata
Harland s.n. C. hildebrandtii
Hassler **10899** C. subternata
——— 8219, 10706 C. affinis
——— 7315 C. sulfurea
——— 1477, **2416**, **7315*b***, 7317, 12390 C. drummondii
——— **5444**, 9376, 10221 C. integrifolia
——— **6011** C. subprostrata
——— **7686, 7686*a*** C. hasslerana
Haught 4352, 4473 C. heterophylla
——— s.n., 40, 191 C. tripartita
Haygarth s.n. C. gerrardii
Hayward 01464, 01465 C. drummondii
Hearn 4 C. hearnii
Heller 1808 C. drummondii
Hemming 2187 C. welshii
Heudelot s.n. C. digitata
Hicken s.n. C. sulfurea
Hildebrandt 780a C. welshii
——— **2325** C. hildebrandtii
Hjalmarson s.n. C. heterophylla
Hoehne 171, 198, 4615 C. affinis
Holmberg s.n. C. argentina
Honold 20 C. digitata
Hooker & T. s.n. C. welshii
Humboldt & Bonpland s.n. C. heterophylla
——— s.n. C. tripartita
——— **593, 1076** C. affinis
Hunziker 1159 C. argentina
——— 11367 C. drummondii
Hutchinson 5 C. gerrardii
Hutchison & Wright 5422 C. tripartita
Ibarrola 944, 2263, 2423, 2556, 2607, 2668 C. sulfurea
——— 2511 C. drummondii
Jeullet 727 C. affinis
Jobert 1037 C. affinis
Johnston s.n., 53175.14, 53175.15, 541181 C. drummondii
Jones 413 C. drummondii
Jorgensen 2316, 3054, 3814 C. drummondii
Jurado 15 bis C. sulfurea
——— s.n., 15 C. drummondii
Kassner 121 C. gerrardii
Kermes 282 C. drummondii
King 394, 1356 C. rosei
Klingberg s.n. C. digitata
Krapovickas 10041, 10042, 10043 C. argentina
——— 261, 348, 743, 992, 1293, 1305, 7818, 7972 C. drummondii
——— 7971 C. sulfurea & C. drummondii (mixed)
——— 7956, 7961 C. sulfurea
——— & Cristóbal 11805 C. ulmifolia
——— 14325 C. drummondii
——— & Ahumada 13945 C. subprostrata
——— 14249 C. hasslerana
Krebs s.n. C. heterophylla
Kuntze s.n. C. drummondii
Landeman 46 C. tripartita
——— 2094 C. affinis
Legagneux s.n. C. digitata

Legname & Cuezzo 3035	C. argentina
Lemos 127	C. hildebrandtii
Leprieur 1	C. digitata
Lewton s.n.	C. drummondii
Liebenberg 3492	C. gerrardii
Lillo 4402	C. argentina
Linden 1456	C. affinis
Lindman A3037	C. affinis
——— A2235	C. drummondii
Lorentz s.n., 253, 571, 883	C. sulfurea
——— 1428	C. sulfurea & C. drummondii (mixed)
——— 1372	C. drummondii
——— & Hieronymus 1082	C. drummondii
——— **384, 1006**	C. argentina
Lukefahr s.n.	C. yucatanensis
Luna s.n., 1037	C. argentina
Lundell & Lundell 8017	C. yucatanensis
Lynch s.n.	C. drummondii
Macedo 372, 4197	C. affinis
Maguire 2183	C. digitata
Maldonado 241	C. argentina
Malme s.n.	C. affinis
— — **1666**	C. cuyabensis
——— s.n.	C. drummondii
Malvarez 1473	C. sulfurea
Martius 1397, 2680, 2681	C. affinis
Maxwell-Darling 94	C. hearnii
Meeuse 9581	C. digitata
Merxmüller & Geiss 1355, 1549	C. digitata
Meyer 21	C. digitata
Meyer, T. 2653, 8792, 10595, 11273	C. sulfurea
——— 684, 2074, 4685	C. drummondii
——— 2075	C. ulmifolia
——— 12798	C. hispida
——— 8368, 21185	C. argentina
Miller & Johnston 66	C. heterophylla
Millspaugh **1693**	C. yucatanensis
Miranda 8551	C. rosei
Mocquerys 960	C. affinis
Moldenke 619	C. yucatanensis
Molfino & Clos s.n.	C. sulfurea & C. drummondii (mixed)
Monetti 14711	C. hispida
Moore 1056	C. drummondii
Morel 33, 734, 896, 1684, 2141, 2192, 2388, 2756	C. drummondii
Moritz 529, 1038	C. heterophylla
——— 98	C. affinis
Morong 929	C. drummondii
Morton A1286	C. heteroclada
Muniez s.n.	C. hildebrandtii
Murdoch 123	C. sulfurea
Müsch 36	C. drummondii
——— 995	C. sulfurea
Myre & Balsinas 1663	C. hildebrandtii
Naboulet 164	C. sulfurea
Nealley s.n.	C. drummondii
Nelson **2779**	C. rosei
Newbould 716	C. somaliana
O'Donell 4715, 4718, 5460, 5482	C. argentina
Olufsen 385*a*	C. digitata
d'Orbigny 86	C. sulfurea
Osten 5407	C. sulfurea
Parsons s.n.	C. gerrardii
Pedersen 4698, 5283	C. sulfurea
——— 477, 4099	C. ulmifolia
——— 5042	C. hasslerana
Pedro & Pedrogão 643-A	C. hildebrandtii & Gossypium sp. (mixed)
——— 663, 2114	C. hildebrandtii
Pedrogão 27, 225	C. hildebrandtii
Perrottet s.n., 32, 66	C. digitata
Pierotti 1, 6, 4226, 4268	C. drummondii
Pilger **289**	C. cuyabensis
Pittier 8143	C. affinis
Plée s.n.	C. heterophylla
Pohl 223	C. affinis
Popov, Tilling & Gilliland 4236, 4277	C. hearnii
Pride s.n.	C. drummondii
Puccioni & Stefanini **617**	C. chiarugii
Raben 886	C. affinis
Ragonese 2089	C. ulmifolia & C. drummondii (mixed)
——— & Piccinini 6554	C. sulfurea
Raunkaier s.n.	C. heterophylla
Rautanen 19, 401	C. digitata
Reales 63, 73, 172, 289, 312	C. drummondii
Rehmann 5223	C. digitata
——— **7128**	C. gerrardii
Richardson 899	C. heterophylla
Riedel s.n., **543**, 2024	C. affinis
Robert 887, 891	C. drummondii
Rodrigo 606	C. sulfurea
Rodriguez 12	C. argentina
Roger 13	C. digitata
Rogers 14561	C. gerrardii
——— 12624, 22389	C. hildebrandtii
Rojas 2592	C. sulfurea
——— **100**, 1935, 8975, 13589	C. drummondii
——— 6207	C. integrifolia
——— 7019*a*, 7179	C. argentina
——— 2599, 5208, 7019	C. ulmifolia
——— 2587	C. hasslerana
Rojas Acosta s.n.	C. sulfurea
Rose s.n.	C. heterophylla
Ruiz 494	C. argentina
Ruyssen s.n.	C. digitata
Saphis 239	C. drummondii
Schenck 825	C. hildebrandtii
v. d. Schijff 2076	C. gerrardii

——— 3409, 3938	C. hildebrandtii
Schinz 212, 213	C. digitata
Schlechter 3950	C. gerrardii
——— 11770	C. hildebrandtii
——— 4664	C. digitata
Schlieben 9248	C. digitata
Schomburkg s.n., 455, **838**	C. affinis
Schott 693	C. yucatanensis
Schreiter s.n., 1549, 5808, 7414, 9439	C. argentina
Schroeter 37	C. sulfurea
Schulz, A. 627, 7978	C. sulfurea
——— 3780	C. drummondii
——— 169	C. sulfurea and C. drummondii (mixed)
——— **170,** 622, 10998	C. ulmifolia
Schulz, C. 305	C. sulfurea
Schulz, E. 2969	C. drummondii
Schwarz 9949	C. ulmifolia & C. sulfurea (mixed)
——— 8700	C. ulmifolia
——— 10084	C. sulfurea
Schweinfurth 75	C. welshii
Sellow **1053**	C. sulfurea
Serié & Mijoya 665	C. sulfurea
Shafer 634, 686, 2639	C. yucatanensis
Sheppard s.n.	C. tripartita
Shiller M5	C. drummondii
Sieber 58	C. digitata
Silva 144	C. affinis
Simpson 469	C. yucatanensis
Sinclair s.n.	C. tripartita
Small, Bailey & Matthaus 11599	C. yucatanensis
G. D. Smith 253	C. affinis
H. H. Smith 779	C. heterophylla
de la Sota 86	C. argentina
Spegazzini 69, 149	C. sulfurea
——— s.n.	C. argentina
Spruce 6393	C. tripartita
Steere 3019	C. yucatanensis
Stephens 1	C. heterophylla
Steyermark 57634	C. heterophylla
——— 55189	C. affinis
——— & Agostini 91287	C. heterophylla
St.-Hilaire s.n., 1021	C. affinis
——— **241**	C. sulfurea
Story 6509	C. digitata
Strey 4028, 4757	C. hildebrandtii
——— 3493	C. digitata
Stuckert 7081, 9679, 9940, 10042, 11558, 21440	C. sulfurea
——— 9128, 12821, 16969	C. argentina
Tatavinow s.n.	C. affinis
Tate 99	C. affinis
Taylor s.n.	C. hildebrandtii
Tharp s.n., 3606	C. drummondii
Thesiger s.n.	C. hearnii
Troll 929	C. argentina
Tyson 1408	C. gerrardii
Ule 7979	C. affinis
Van Fleet 6095	C. drummondii
Van Landsberge 249	C. affinis
Velasco 7	C. affinis
Ventenat s.n.	C. heterophylla
Venturi 551, 5678	C. drummondii
——— 7370, 8761	C. argentina
——— **10311**	C. hispida
——— 190	C. ulmifolia (see also C. drummondii)
——— 190 bis	C. ulmifolia
Vidal-Sénège s.n.	C. tripartita
Villalón s.n.	C. argentina
Volk 125	C. digitata
Wagener 76	C. heterophylla
——— 350	C. affinis
Wall 37	C. argentina
Walter 2/187, 429	C. digitata
Ward 3240	C. hildebrandtii
Waring 19	C. welshii
Warming s.n., 442	C. affinis
Weberbauer 4262, **6214**	C. tripartita
Weddell 2641	C. affinis
Wells 2048	C. hildebrandtii
Welti 17	C. digitata
West 8396	C. argentina
White **1538**	C. affinis
Williams 13585, 13646	C. affinis
Wilms 83, 83a, 83b	C. gerrardii
Wolcott & Barkley 16T416	C. drummondii
J. M. Wood 239, 11722	C. gerrardii
R. C. Wood s.n., 6828	C. hildebrandtii
Woronow 7528	C. affinis
Wulfhorst 21	C. digitata

Index to Latin Names

New taxa are in **boldface**, all other taxa are in roman type; numbers in **boldface** refer to descriptions, numbers in roman refer to synonyms, and numbers with dagger (†) refer to names mentioned incidentally.

Abelmoschus esculentus 182†
Acacia barbertonensis 198†
Alabama argillacea 182†
Alyogyne cuneiformis 241†; hakeaefolia 241-242†
Anthonomus grandis 183†
Bombacaceae 179†
Bouteloua 182†; aristidoides 182†; barbata 182†
Cephalohibiscus 179†, 181†
Cienfuegia 180†, 191
Cienfuegosia **191**; subg. **Articulata** 183†, 187†, 189-191†, **194**, 198†; sect. **Articulata** 183†, 187†, 189†, **194**; sect. **Dioica** 183†, 194†, **203**, 203†; sect. **Garkea** 183†, **196**; sect. Synodontos *(nom. nud.)* 196†, 202†; subg. **Cienfuegosia** 183†, 187†, 189-191†, **204-205**, 205†, 217†; sect. **Cienfuegosia** 183†, 186-187†, 189†, 192†, **205**, 205†, 217†; sect. **Friesia** 181-184†, 187†, 189-190†, 192†, 204†, **228-229**, 229†; sect. **Paraguayana** 183-184†, 187†, 189-190†, **220-221**, 221†; sect. **Robusta** 183-184†, 189†, **216**, 216†; affinis 181-183†, 189†, 191-192†, 204†, **216-217**, 216-218†, var. campestris 217, var humilis 217, 241†; althaeoides 241; anomalum 241; argentina 181-182†, 187†, 190-191†, **229-230**, 229-230†, 234†, var. hasslerana 229†, 237, f. escholtzioides 229†, 237; australis 241, var. microcarpa 241; benthamii 241, 241†; bricchettii 241; chiarugii 183†, 187†, 189†, 196†, **202**; cuneata *(nom. nud.)* 242†; cuneiformis 241; cuyabensis 189†, **219-220**, 220†; digitata 183†, 186†, 189-192†, 205†, **206**, 206-208†, var. lineariloba 206, 207†; dinteri *(nom. nud.)* 242†; drummondii 182†, 184-185†, 187†, 190 192†, 221-222†, **223-224**, 224-226†, var. genuina 223, 241†, var. pubescens 221; ellenbeckii 241; escholtzioides 237, 237†; flaviflora 241; gerrardii 183†, 187†, 189†, 192†, **194-195**, 194†, 198†; gossypioides 241; hakeaefolia 241, var. lilacina 241; hasslerana 190†, **234**, **237**, 237†; hearnii 182-183†, 187†, 189†, 191-192†, **202-203**, 203†; heteroclada 183†, 187†, 189†, 191-192†, 203†, **204**, 204†, 228†; heterophylla 182†, 186-187†, 189-191†, 205†, 209-210†, **211**, 212†, 215†, ssp. subternata 212, var. cuneata 213, 215†; hildebrandtii 181-183†, 189-190†, 192†, 196†, **197**, 198†; hispida 182†, 190†, 229†, **231**, 231†; incana 241; integrifolia 183†, 190†, **227-228**; intermedia 189†, 215†, **220**; junciformis 206, var. ruyssenii 206; latifolia 241; palmeri 241; pedata 241; pentaphylla 241; phlomidifolia 216, var. humilis 210†, 217, 241†; populifolia 242; pulchella 242; punctata 241†, 242; riedelii 217, 218†; robinsonii 242; **rosei** 183†, 186-187†, 189†, **210**, 210†, 212†; somalensis 242; somaliana 187†, 189†, 191-192†, 196†, **200-201**, 200-201†; subprostrata 189-190†, **228**, var. vera 227, 227†, 241†; subternata 186†, 189†, 205†, **212-213**; *sulfurea (Juss.) Garcke 182†, 187†, 190-191†, 216, **221-222**, 221-222†, 224-225†, var. drummondii 223, var. genuina 221, var. glabra 223, 223†, f. intermedia 223, var. integrifolia 227, var. major 223; sulphurea Garcke *emend.* Robins. 223; sulphurea Hassl. 216, 241†; thespesioides 242; tripartita 183†, 186-187†, 189†, 191-192†, 204†, 210†, **213**, **215**, 215†; triphylla 242; ulmifolia 182†, 189-190†, 222†, 225†, **234**; welshii 183†, 187†, 189†, 191-192†, **199-200**, 200-201†; yucatanensis 182-183†, 186-187†, 189-191†, 205†, **208-209**, 209†
Cienfugiosa 180†, 191
Cienfugosia 180†, 191
Diparopsis castanea 183†; **telephragramma** 183†; watersi 183†
Elidurandia 180†, **191**; texana 180†, 223, 225†
Fugosia 180†, 191, 224†, 241†; affinis 216; areysiana 242; argentina 229; australis 242; campestris 216; cuneata 213; cuneiformis 241; digitata 206, 208†; drummondii 223, 225†; flaviflora 241; gerrardi 195; grantii 242; guianensis 217; hakeaefolia 241, var. coronopifolia 242; heteroclada 204; heterophylla 211; hildebrandti *(nom. nud.)* 242†; lanceolata 216, 218†; latifolia 241; lilacinus 241; pedata 241; phlomidifolia 216; populifolia 242; pulchella 242; pulverulenta 223; punctata Turcz. 211, 212†, 241-242; punctata Cunn. ex Benth. 211†; retusa 217; robinsonii 242; *sulfurea 221, var. trifida *(nom. nud.)* 223, 242†; thespesioides 242; tripartita 213; triphylla 242; welschii 199
Gossypieae 179-181†, 187†, 204†
Gossypioides 179†, 181†

Gossypium 179†, 181-183†, 186-187†, 190†, 192†, 200†, 203†; anomalum 183†, 186†, 241†; areysianum 242†; aridum 241†; australe 198†, 241†; bickii 241†; costulatum 241†; cunninghamii 241-242†; herbaceum var. dinteri 242†; incanum 241†; populifolium 242†; pulchellum 242†; robinsonii 242†; somalense 208†, 241-242†; sturtianum 241†; triphyllum 242†
Hampea 179†, 181†, 187†, 190†, 204†
Hibisceae 179†, 181†
Hibiscus 181†, 187; sect. Furcaria 181†; affinis 216; acetosella 182†; argentinus 229; bifurcatus 181†; campestris 217; cavanillesianus 206†; cavanillesii 206; cuneata 213; drummondii 223; esculentus 182†; hilairei 216; jussieui 221; ludwigii 241; phlomidifolia 216; pulverulentus 223, 223-224†; radiatus 182†; rectiflorus 217; redoutei 211; rubidus 181†; sulphureus 216, var. acutifolius 216; tripartita 213; welshii 199
Kokia 179†, 181†
Kosteletzkya grantii 242†
Kydia 187†
Lebronnecia 179†, 181†
Malvaceae 179†, 187†
Napaea 187†
Puccinia stakmanii 182†
Redoutea 180†, 191; heterophylla 211†; tripartita 180†, 213, 215†
Redutea 180†, 191; heterophylla 211
Sacadodes pyralis 183†
Thespesia 179†, 181†, 190†; lampas var. thespesioides 241-242†; multibracteata 181†; rehmannii 195

*The alternate spellings of Jussieu's epithet, *sulfurea* and *sulphurea*, are not separated in this index.

THE INITIATION OF VASCULAR CAMBIUM AND PRODUCTION OF SECONDARY XYLEM IN FLOWER BUD PEDICELS OF *ASCLEPIAS CURASSAVICA* L. IN CULTURE[1]

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ABSTRACT

Flower buds of *Asclepias curassavica* were cultured to determine the effects of indole-3-acetic acid (IAA) and kinetin (6-furfurylaminopurine) on the secondary growth of the pedicels. Initiation and activity of the cambium were achieved on media containing both of these substances as well as on media containing 1 mg/l auxin and 10 mg/l autoclaved deoxyribonucleic acid (DNA). The highest cambial activity and secondary xylem production occurred in pedicels grown on the latter medium. This study suggests that the presence of IAA and kinetin together in the medium enhances the mobility of both, and that there is an interaction between auxin and kinetin in initiating vascular cambium and influencing its subsequent activity. Such an interaction may also take place in the pedicels of fruit of *Asclepias curassavica* undergoing secondary growth.

INTRODUCTION

The flower pedicels of many plants are herbaceous and consist entirely of primary growth. However, following pollination, fertilization, and the subsequent development of fruit, they very often undergo considerable thickening and become quite woody. Such a change in the habit of the pedicels of some plants has been attributed to the effects of auxins (Nitsch, 1952, 1965). Auxins are known to occur in relatively large quantities in the developing fruits of a number of plants (Nitsch, 1950; Wright, 1956; and others), and it is conceivable that they play a role in the secondary growth of pedicels. This hypothesis is further supported by the fact that auxins induce cambial initiation and xylem differentiation, both in tissue cultures (Camus, 1949; Wetmore and Sorokin, 1955; and others), and in intact plants (Jacobs and Morrow, 1957).

Since the classic work of Skoog and Miller (1957), it has become increasingly apparent that the processes of organ and tissue differentiation in plants are influenced by interactions between various growth substances. There is experimental evidence, for instance, that kinins interact with auxins in initiating cambial activity in radish roots grown in culture (Loomis and Torrey, 1964; Torrey and Loomis, 1967) and in pea epicotyl segments (Sorokin et al., 1962).

Cytokinins are known to occur in relatively large quantities in the developing fruits of a number of plants investigated (Steward and Simmonds, 1954; Goldacre and Bottomley, 1959; Letham and Bollard, 1961; Letham, 1967; Nitsch and Nitsch, 1961), but their effects on the secondary growth of pedicels have not been previously reported.

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I first became interested in this problem while culturing flower buds of *Asclepias curassavica*. I noticed that the flower bud pedicels showed signs of lateral growth after growing for several weeks on White's basic medium plus 1 mg/l indole-3-acetic acid (IAA) and 10 mg/l autoclaved deoxyribonucleic acid (DNA), but flower bud pedicels showed little or no secondary growth when grown on White's medium to which only 1 mg/l IAA had been added. This observation led me to explore the possible interaction of kinetin (6-furfurylaminopurine) and IAA in the initiation of vascular cambin and the secondary growth of the pedicels, since autoclaved DNA, in combination with IAA, is known to produce effects similar to that of kinetin in inducing cell division in tissue cultures (Miller et al., 1955).

MATERIALS AND METHODS

Excised young inflorescences of *A. curassavica* were sterilized for five minutes in a mixture of equal volumes of 70% ethyl alcohol and a saturated aqueous solution of calcium hypochlorite. (By using the mixture instead of the two solutions separately, we were able to reduce contamination of the cultures to about 2%.) The inflorescences were then rinsed four times in sterile glass-distilled water, and buds that were three to four mm long with pedicels about one-third of this length were excised. The entire sequence of sterilization and rinsing was performed under a hood and the buds were kept in petri plates placed in an ice bath until they were aseptically transferred onto the appropriate media.

The media used in these experiments consisted of the following:

1. White's basic medium without the added growth substances (White, 1963).
2. White's basic medium and IAA in concentrations of 0.5, 1, and 2 mg/1.
3. White's basic medium plus kinetin (6-furfurylaminopurine) at concentrations of 0.5, 1, and 5 mg/l.
4. White's medium plus a constant concentration of kinetin at 0.5 mg/l and IAA at the various concentrations of 0.5, 1, and 2 mg/l.
5. White's basic medium plus 10 mg/l of DNA and 1 mg/l IAA.

White's basic medium and DNA were autoclaved for 20 minutes under 15 pounds of pressure. Kinetin and IAA were sterilized by Millipore filtering and then added aspectically to the media. 1% Difco agar was added to all media, and the pH was adjusted to 5.5. The media were poured into 30 ml Falcon plastic tissue culture bottles. Eight buds were transferred aspectically onto each of the media, and four replicas were made of each experiment. The bottles were then

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Fig. 1-5. Fig. 1. A flower bud of *Asclepias curassavica* before culturing (× 22). Fig. 2. A flower bud after growing for four weeks on White's basic medium plus 1.0 mg/l IAA. Note the swelling of the basal portion of the pedicel (× 22). Fig. 3. A flower bud after growing for four weeks on White's basic medium plus 1.0 mg l IAA and 0.5 mg l kinetin. Notice the uniform growth of the pedicel. Fig. 4. Transverse section of the pedicel of a young bud before culturing; notice the amphiphloic siphonostele in the center and the poor differentiation of the xylem elements (× 150). Fig. 5. Transverse section of a callus showing nests of vascular tissues and the origin of a root (× 140).

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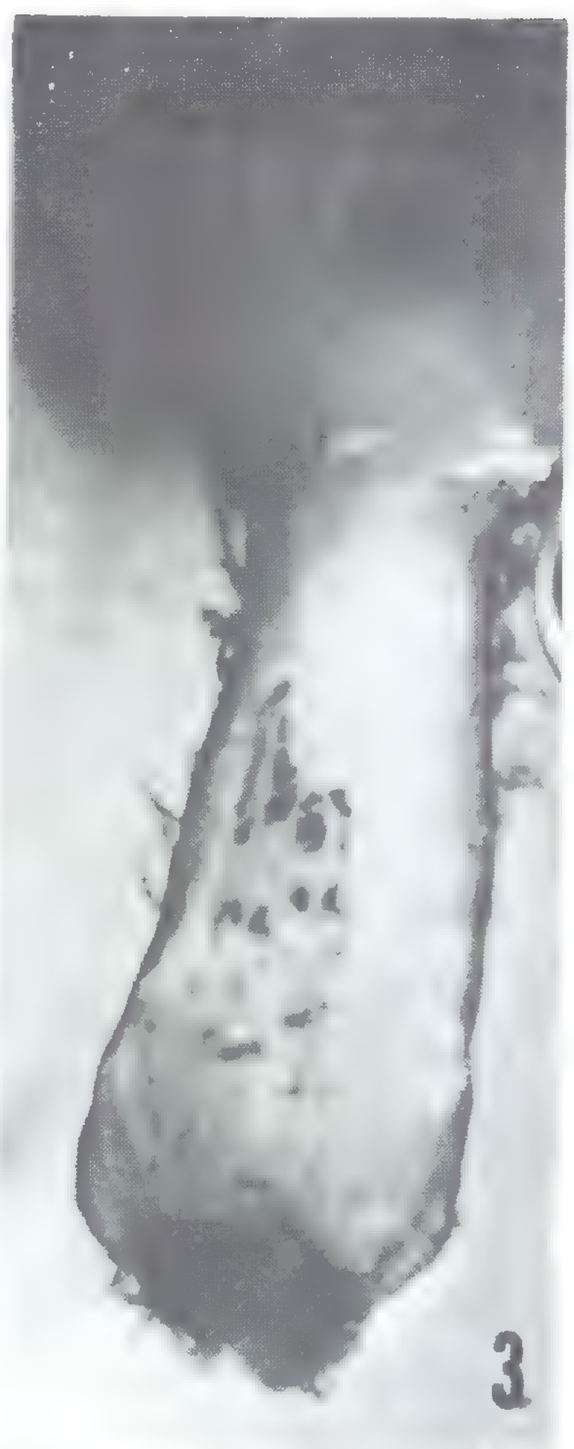

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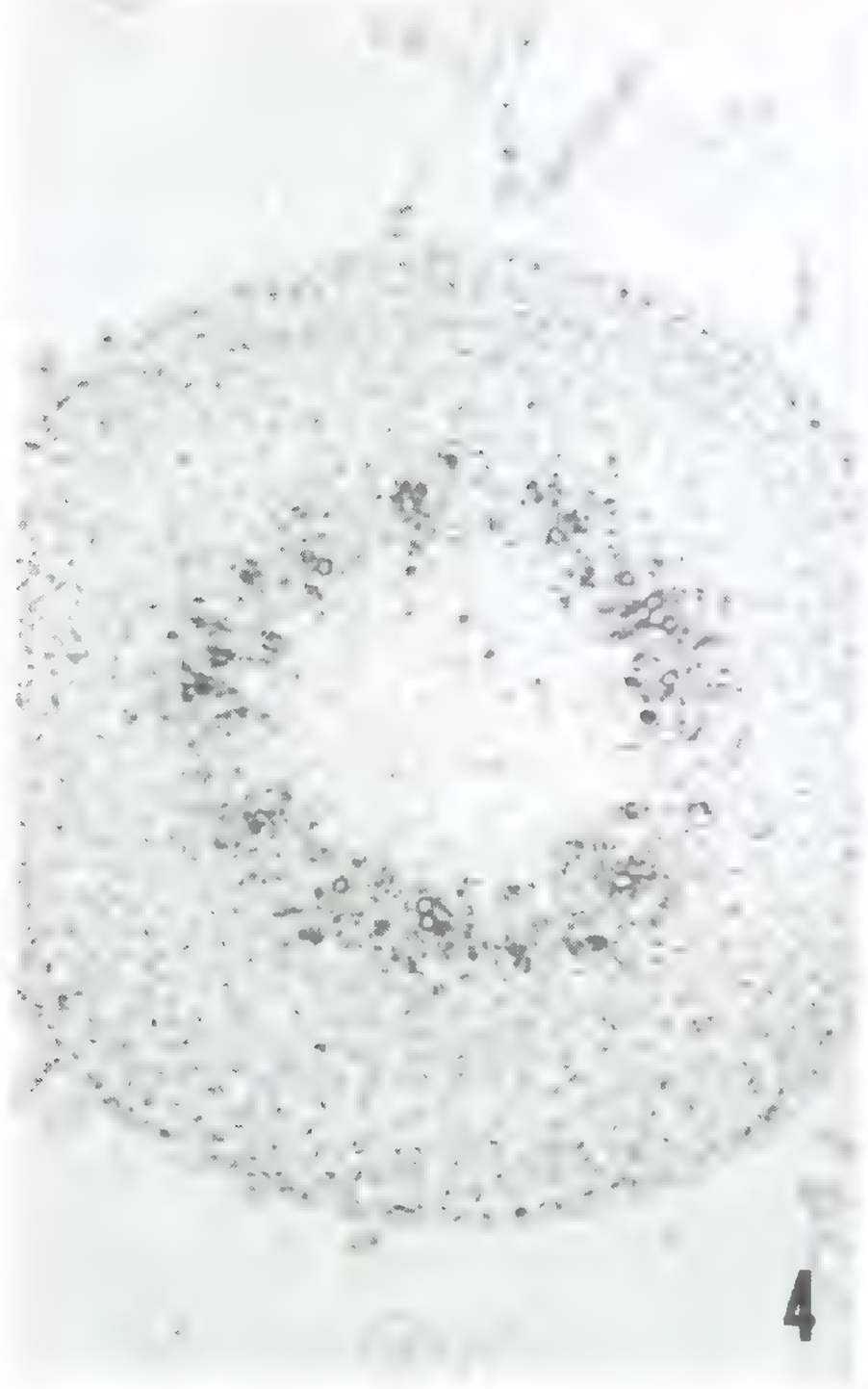

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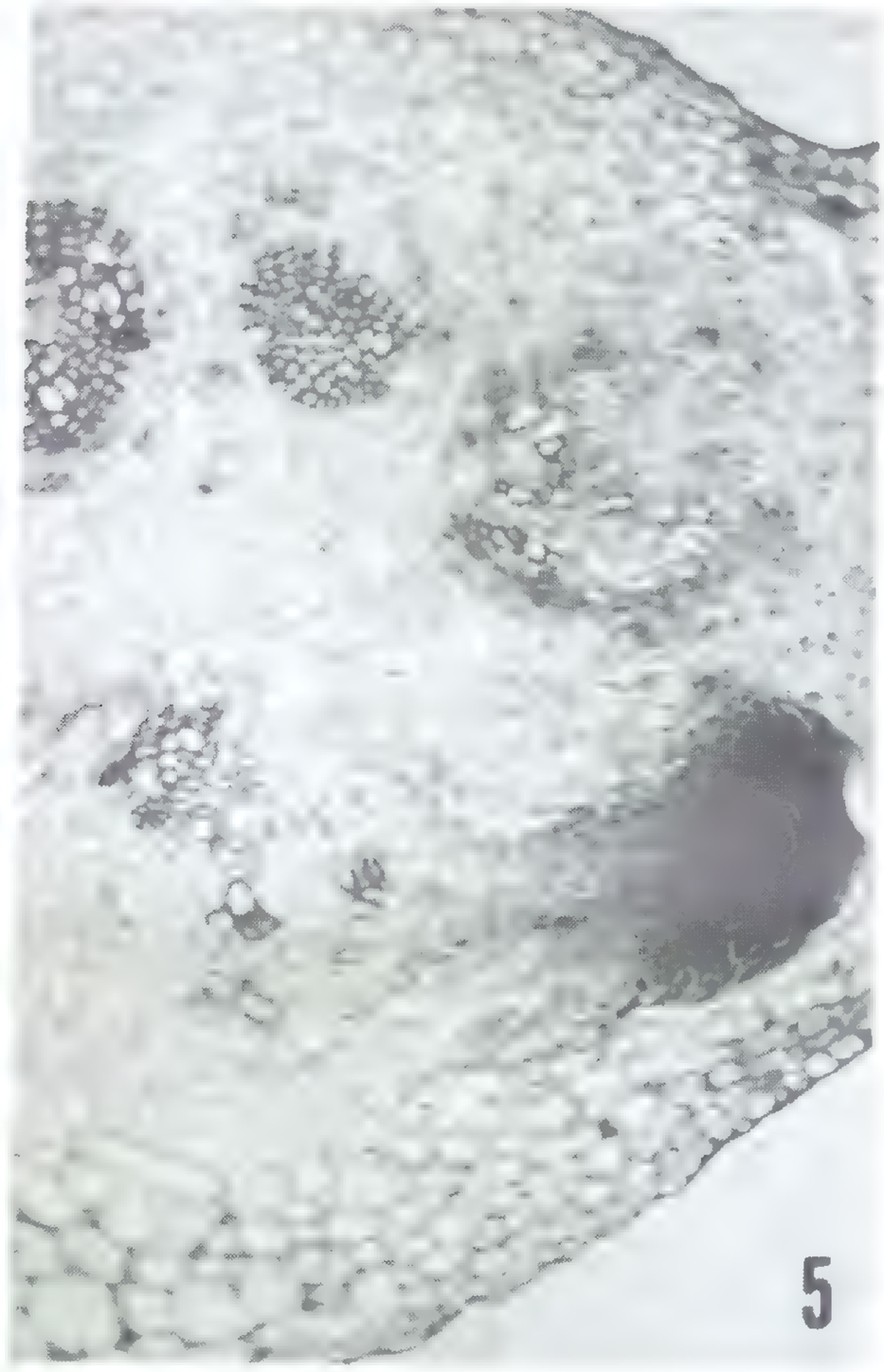

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placed in a growth chamber having a day temperature of 25 ± 1° C. and a night temperature of 20 ± 1° C.; the light intensity was set at 500 foot candles for 12 hours daily. After being kept in culture for periods from two to six weeks, the buds were measured, killed and fixed in formalin-acetic acid-alcohol (FAA) solution.

The preserved material was embedded in paraffin, either by the standard alcohol-xylene method, or by the tertiary butyl-ethyl alcohol procedure. Microtome sections were cut at 10-20μ. Aqueous crystal violet and erythrosin in clove oil produced satisfactory staining that rendered vascular tissues quite distinct. Fast green in 95% ethyl alcohol and 1% aqueous safranin were also used.

Observations and Results

1. *Anatomy of the Pedicel.*

The pedicels of a young bud of *Asclepias curassavica* is terete and has an amphiphloic siphonostele similar to the pedicels of other asclepiad flowers (Safwat, 1962) and corresponds to that of a young stem of the plant. The xylem is embedded in a cylinder of protophloem parenchyma (Fig. 4).

The vascular cylinder appears dissected and not continuous because certain provascular cells have not been differentiated into xylem elements. The pedicel wood consists primarily of protoxylem elements having relatively poor development of the metaxylem. No vessels are apparent, and the secondary walls of the tracheids are either spiral or annular.

During the development of the bud, the pedicel elongates; the cessation of this elongation marks the completion of the metaxylem development. Unlike the young stem, the pedicel contains no fibers.

2. *Experimental.*

Buds placed on the White's basic medium did not grow satisfactorily and showed signs of yellowing in approximately two weeks. There was some elongation of the pedicels, but they did not grow laterally, nor did they form noticeable calluses. The cross sections of these pedicels resembled those of intact buds.

Pedicels of buds grown in the auxin medium elongated to almost double their initial length. The cut ends of these pedicels began to form calluses within two weeks, and a conspicuous swelling occurred during this period (Fig. 2). The buds were sustained in culture for about four weeks, after which time most began to yellow and some died in culture. Both serial cross and serial longitudinal sections revealed vascular differentiation in the callus. Near the base of the callus there was a random distribution of vascular tissues, and, at a slightly higher level, sev-

Fig. 6-9. Portions of transverse sections of pedicels grown on White's basic medium plus 0.5 mg/l kinetin and 1.0 mg/l IAA, showing the ontogeny of cambial initiation and activity. Fig. 6. The lignification and further differentiation of primary xylem elements (× 130). Fig. 7. The initiation of the vascular cambium near the primary xylem (× 130). Fig. 8. The further development of the vascular cambium and the production of secondary wood (× 400). Fig. 9. The origins of the two vascular cambia as observed in a few specimens (× 150).

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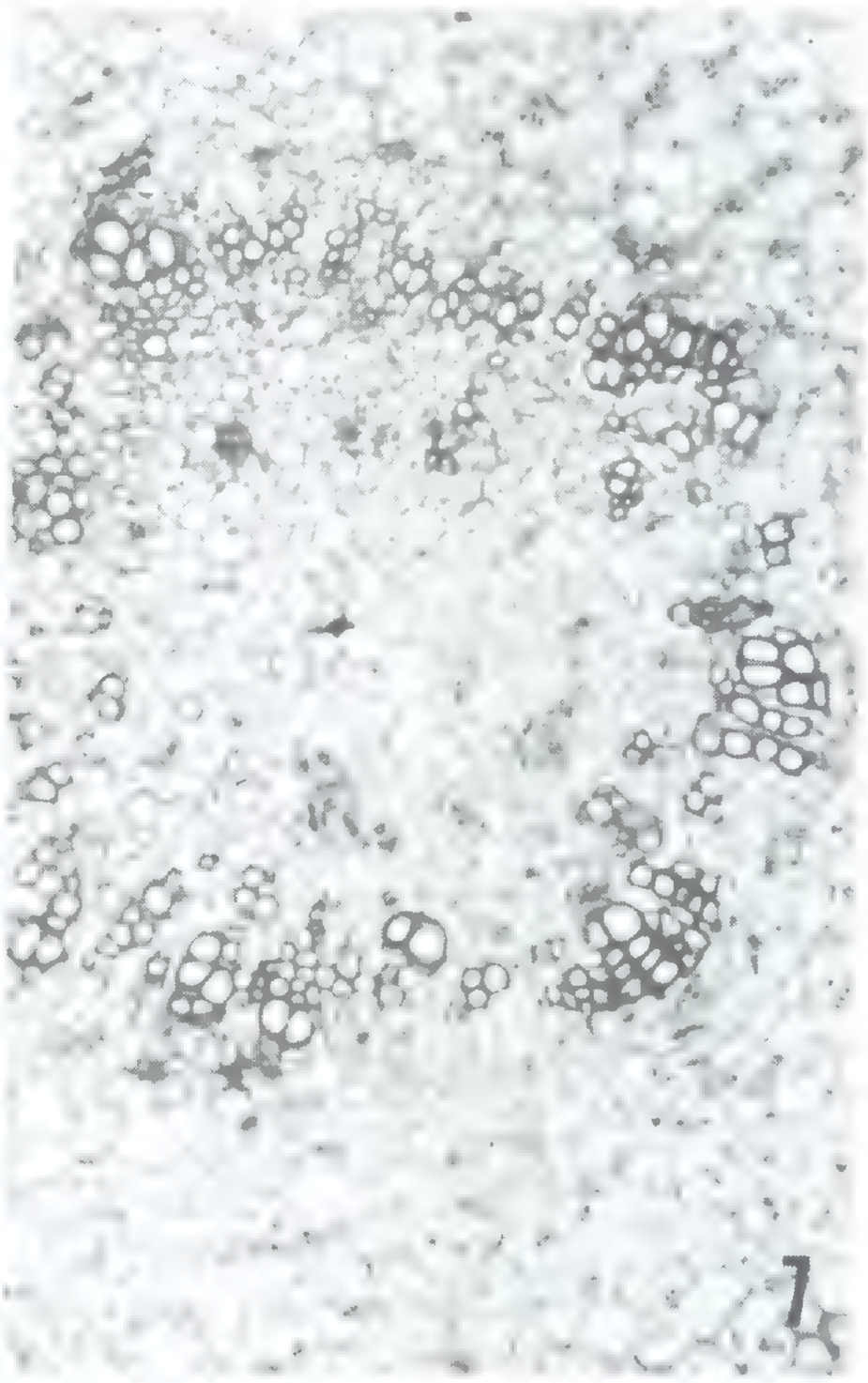
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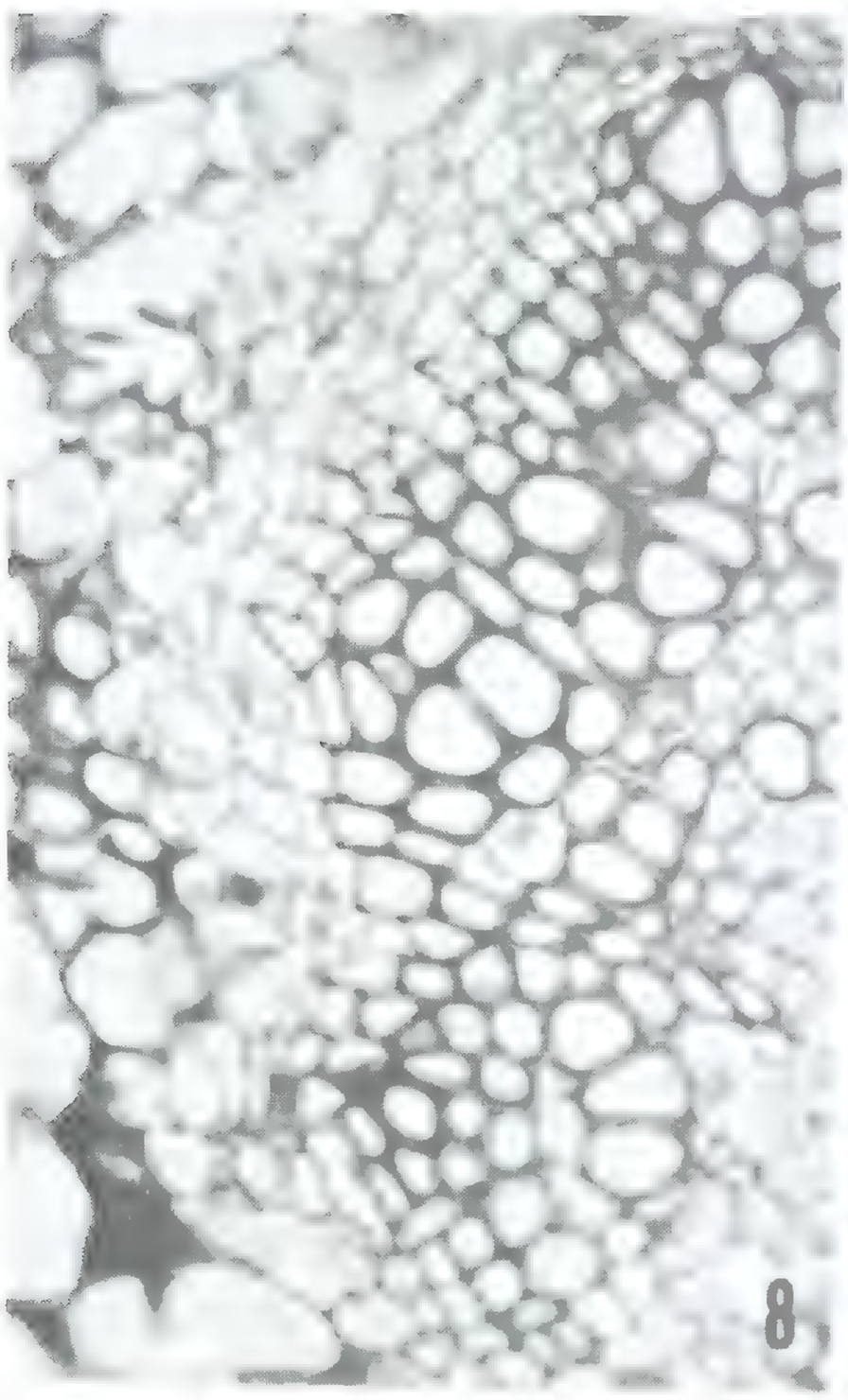
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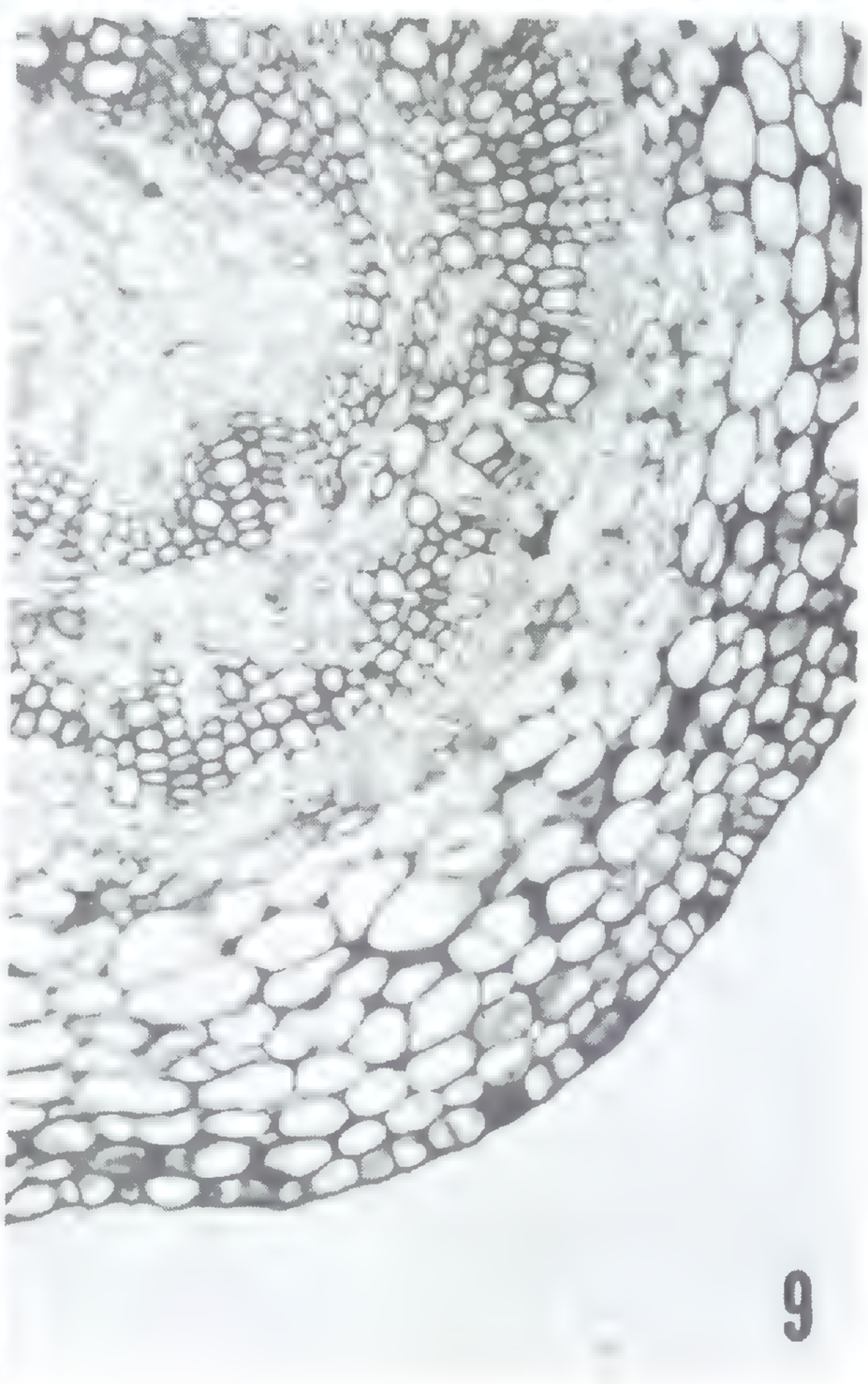
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eral nests of vascular tissues were observed, each nest surrounded by its own meristem. In some pedicels, roots originated from these meristems (Fig. 5). At a still higher level, in the pedicel proper, cambial initiation was noticed in a very few specimens, but the amount of xylem produced was very limited. The cambial activity was confined to the lower one-third of the pedicel in all the specimens examined. The increase of the concentration of IAA from 0.5 mg/1 to 2 mg/1 did not change the cambial activity appreciably.

The growth of buds in the kinetin medium was generally poor; slight elongation of the pedicels was noticed, but with no signs of cambial initiation or activity. The buds were maintained on this medium for about three weeks.

The auxin-kinetin medium supported the growth of sepals and petals (the gynostegium failed to grow on any of the media), and the buds were maintained in culture for a maximum of six weeks. The pedicels elongated and calluses were produced at their cut ends (Fig. 3). The anatomy of the callus was very similar to that of the callus produced on the auxin medium. Nests of vascular tissues were observed; root development occurred in only a few specimens.

3. *Initiation and activity of the vascular cambium in pedicels grown on the auxin-kinetin media.*

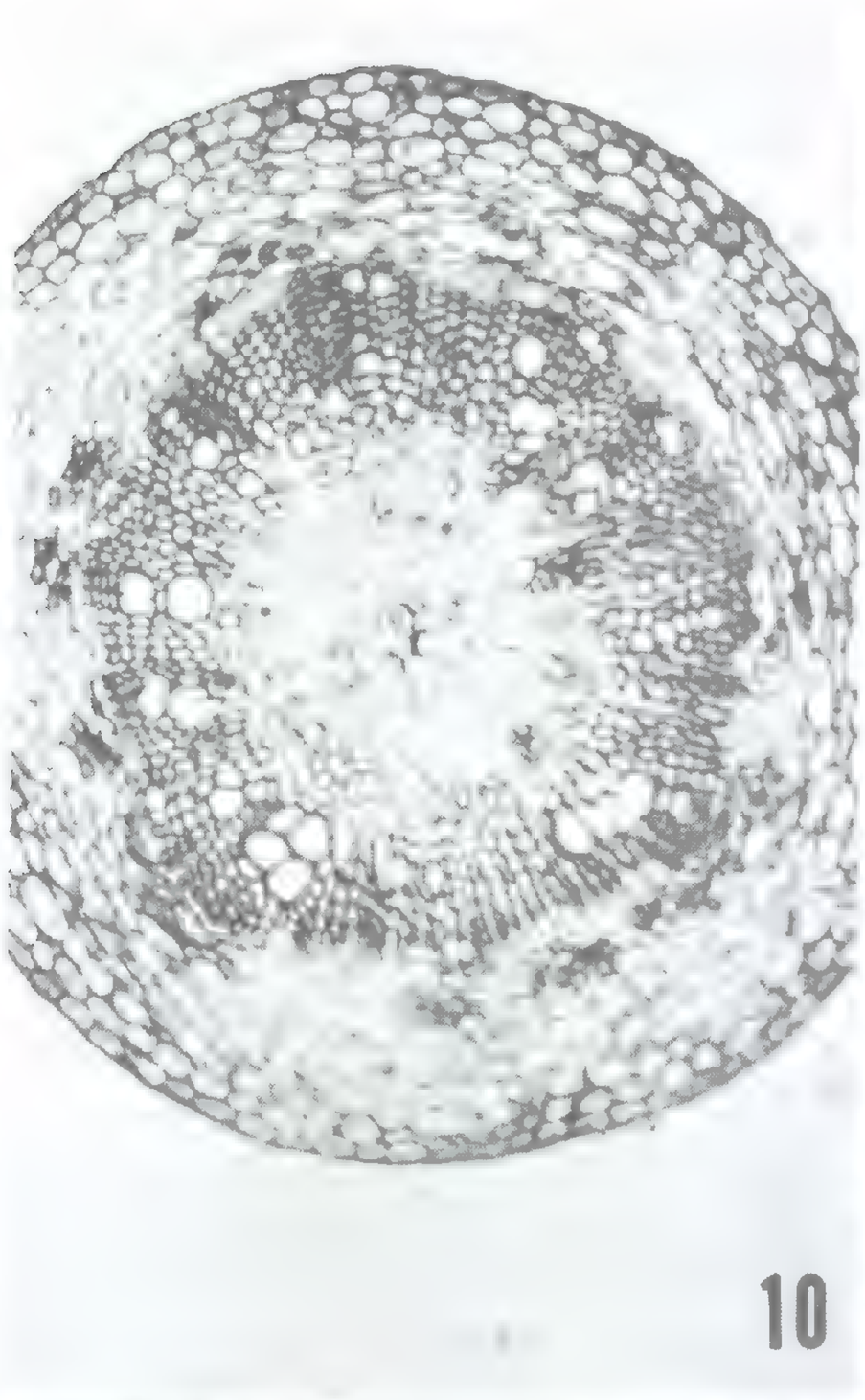
The initiation of cambial activity takes place at a level above the callus within the pedicel proper, and gradually progresses toward the opposite end. In none of the buds examined did cambial activity extend over the entire length of the pedicel.

The first sign of differentiation begins with the development of the metaxylem and the strong lignification of the xylem elements (Fig. 6). Then a vascular cambium originates from parenchyma cells between the primary xylem and the phloem. Cambial formation begins outside the xylem elements, gradually extending tangentially so that a complete layer of cambium is finally produced (Figs. 7 and 8). From this cambium, secondary tissues are derived in a manner similar to their production in stems. In the periphery of the secondary phloem, patches of fibers are seen.

The cork cambium originates from a subepidermal layer and is, therefore, considered to be superficial in origin. Lenticels were also observed in a number of specimens.

In a few pedicels, I encountered a different pattern of cambial activity in which two distinct cambia arose. The first of these originated as described above while the second was derived from the activity of the inner phloem region and produced xylem centrifugally and phloem centripetally (Fig. 9). When two cambia arose, only the outer one continued its activity, whereas the inner cambium ceased functioning after an initial production of secondary xylem. In stems having

Fig. 10-13. Fig. 10. Transverse section of a pedicel after growing for five weeks on White's basic medium plus 1.0 mg/l IAA and 10 mg/l autoclaved DNA; notice the proportion of the secondary xylem to the rest of the section (×110). Fig. 11. A portion of Fig. 10 at a higher magnification (×400). Fig. 12. Longitudinal section of a pedicel showing vessels and tracheids (×400). Fig. 13. Transverse section of a young stem of *Asclepias curassavica;* notice the relative amount of secondary xylem compared with the rest of the section (×100).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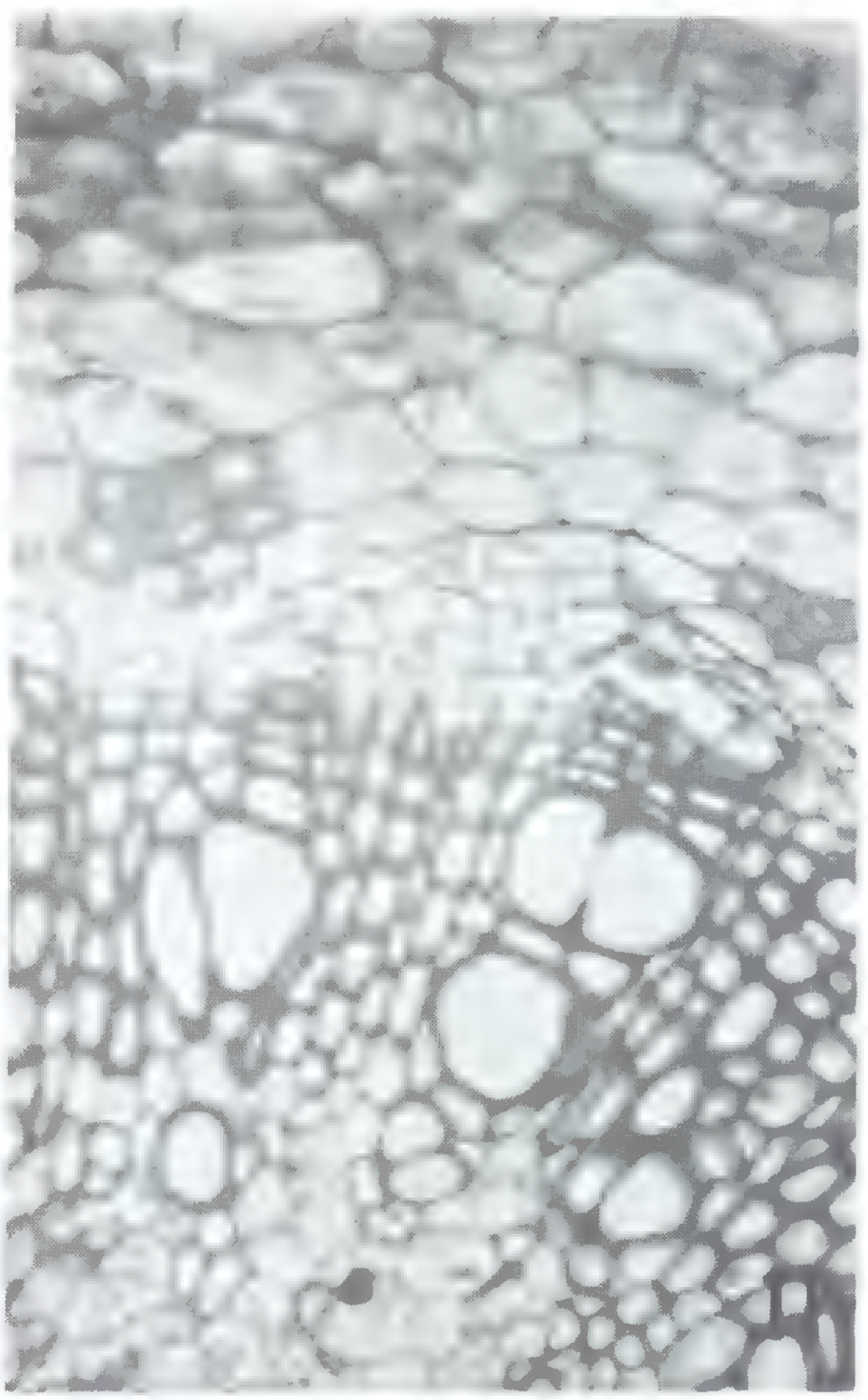
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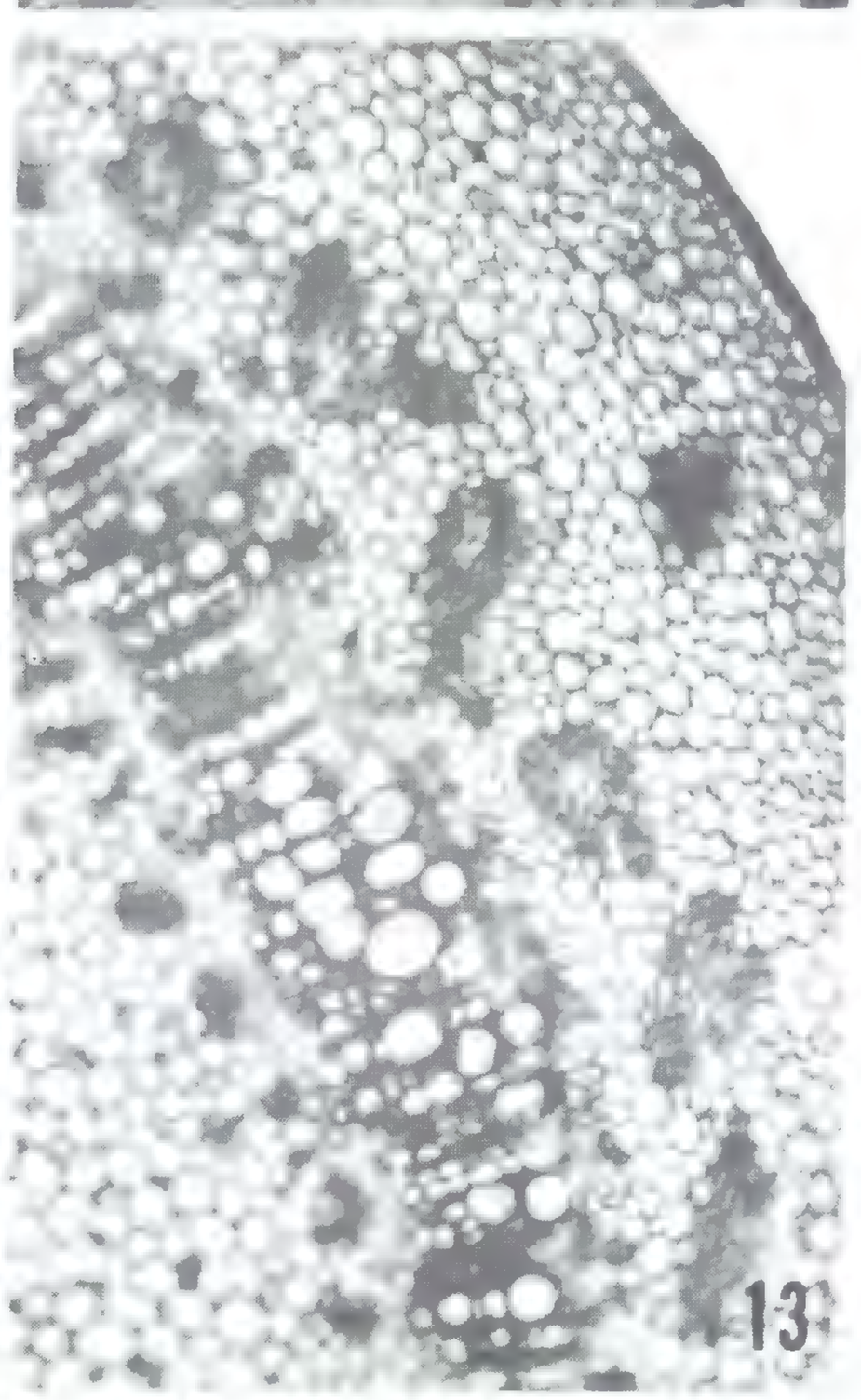
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amphiphloic steles — such as, tobacco, potatoes, and tomatoes — one cambium normally originates and from the outer phloem alone (Esau, 1960).

In all specimens the secondary wood consists of tracheids and vessels, the latter having simple perforations and measuring 150-200μ in diameter (Fig. 12). Pittings on the secondary walls of the vessels were alternate. In general, cells of tissues in pedicels are larger than their counterparts of intact plants.

In none of the experiments was the secondary xylem production as spectacular as in pedicels grown on a medium containing 10 mg/l autoclaved DNA and 1 mg/l IAA. On this medium the pattern of initiation and activity of the cambium was similar to that observed in pedicels grown on the auxin-kinetin media, but the amount of secondary wood was most remarkable. In Figure 10 notice the proportion of the xylem to the rest of the pedicels. When this is compared with a cross section of a young stem of the same plant measuring about 3 mm in diameter (Fig. 13), the extent of the cambial activity in the pedicel is quite apparent.

DISCUSSION

The effects of auxins on the stimulation of cambial activity and xylem differentiation have been reported by a number of investigators (Camus, 1949; Wetmore and Sorokin, 1955; Jacobs and Morrow, 1957; and others). However, it seems that auxin alone is not sufficient for the initiation and subsequent activity of the vascular cambium, at least not in bud pedicels grown in vitro. Thus, in this series of experiments, the differentiation of the vascular cambium of buds grown on media containing only IAA either did not occur at all, or, when present, the secondary xylem formation was very limited. This is in sharp contrast to cambial activity in pedicels grown in the kinetin-auxin or the DNA-auxin media.

It seems that in buds grown on media containing auxin alone, the auxin tended to be localized in the callus as is indicated by the swellings of this region. This is similar to the situation of callus swellings on plants following the application of auxin (Leopold, 1964). The presence of kinetin or DNA in addition to the auxin seems to cause a more uniform growth of the pedicel.

It is possible that kinetin is involved in increasing the mobility of the auxin. Kinetin by itself is poorly translocated in plant tissues (Miller, 1961). But a number of investigators have shown that kinins enhance the mobility of auxins in plants (McCready et al., 1965), and that auxin may, in turn, increase the mobility of kinetin (Seth et al., 1966). Therefore, it seems probable that auxins and kinens increase the translocation of each other (McCready, 1965).

Such an increase in the auxin and kinetin mobility may also be operational in the pedicel. One evidence for this conclusion is the swelling of the callus in the absence of kinetin. Further experiments are now underway to determine the possible interdependence of the translocation of these growth substances in the pedicel.

The interaction between kinins and auxins in differentiation has been stressed by Skoog and Miller (1957); and by Torrey and Loomis (1964, 1967) who showed experimentally that kinetin is very important in the initiation and activity

of the vascular cambium of excised roots of radish grown in culture. Such an interaction is also reported by Sorokin et al. (1962) in the pea epicotyl segments.

There is a strong possibility that kinetin and auxin are required for the initiation and activity of the vascular cambium in the pedicels. Kinetin alone did not support the growth of pedicels and IAA without kinetin produced very limited cambial activity and in only a few of the buds. Such activation may be a result of the presence of some endogenous kinins in the buds when they were excised.

It may be concluded that, in addition to the probable increase in the mobility of the auxin and kinetin, there seems to be an interaction beween the two growth substances leading to cambial initiation and wood production in the pedicel. Although 0.5 mg/l of kinetin and 1 mg/l of IAA showed "good" cambial activity, no optimum concentrations of these substances have been established for cambial activity in bud pedicels. However, preliminary observations indicate that increasing the concentrations of kinetin and IAA to 1 mg/l and 2 mg/l, respectively, seems to increase the cambial activity in bud pedicels.

The fact that flower pedicels of intact plants do not show signs of lateral growth is probably because insufficient quantities of these substances are produced. On the other hand, both auxins and cytokinins are known to occur in relatively large quantities in developing fruits of a number of plants. This may also be true in the development of *Asclepias* fruits. Further experiments will be conducted to explore the possibility of the interaction of kinins and auxins in the secondary growth of fruit pedicels in various species of *Asclepias*.

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CYTOLOGICAL AND CHROMATOGRAPHIC EVIDENCE FOR INTERSPECIFIC HYBRIDIZATION IN PETALOSTEMON[1]

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ABSTRACT

Chromatographic profiles of flavonoid extracts of *P. purpureum* and *P. gattingeri* are quite distinct, *P. purpureum* showing 12 species-specific compounds, and *P. gattingeri* showing 6 specific compounds. Chromatographic profiles of all putative hybrids except one exhibit compounds specific to each parental species. Three types of chromosomal abnormalities exist in putative hybrids which are not present in either parental species, but completely normal meiosis is reported in several hybrids.

In a revision of the genus *Petalostemon* Michx., Wemple (1965) reported that interspecific hybridization is possible within taxonomic sections of this genus but not between species of different sections. He created fertile, artficial hybrids between *Petalostemon gattingeri* (Heller) Heller and *P. purpureum* (Vent.) Rydb., members of sect. *Purpurei*. In nature, these species are usually ecologically isolated. *Petalostemon gattingeri* is endemic to limestone glades in Tennessee and Alabama, and *P. purpureum* is a prairie species.

In the central basin of middle Tennessee, *Petalostemon gattingeri* is widespread on limestone glades, while only a few individuals of *P. purpureum* have been found in the area. Naturally occurring populations of putative hybrids of these two species were observed by Breeden (1968) in Cedars of Lebanon State Park in Wilson County, Tennessee. In these populations, *P. gattingeri* was found along a roadside and on patches of open limestone. *Petalostemon purpureum* was found in adjacent areas which Breeden considered to be prairie relicts. He measured fourteen morphological characters of the two parental species and of putative hybrids and found that the hybrids were generally intermediate between the two parental species or within the range of variation of one of them. The present study was undertaken to supplement morphological data with chromotographic and cytological data.

MATERIALS AND METHODS

The following populations of the parental species and hybrids were studied:

P. gattingeri

Davidson County, Tennessee: Mount View. *Walker 195*

Davidson County, Tennessee: Couchville Pike. *Walker 196.*

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P. purpureum

Sevier County, Arkansas: Ben Lomond. *Demaree* 53998.

P. purpureum × *gattingeri*

Wilson County, Tennessee: Cedar Forest Road. *Walker 176.*

Wilson County, Tennessee: Hurricane Creek Road. *Walker 190.*

Voucher specimens from these populations are deposited in the Vanderbilt University Herbarium (VDB).

Chromatography. Chromatographic patterns of flavonoid compounds in the two parental species were established from plants collected from pure populations in which there was no evidence of hybridization. Ten plants of each parental species and ten plants from each of the two putative hybrid populations were analyzed. Flavonoid compounds were extracted from stems and leaves in 99% methanol : 1% normal HCl in a ratio of one gram dry weight of plant material : ten ml. extracting solvent. Twenty drops of extract were spotted on a sheet of Whatman #3 MM chromatographic paper which was developed in the first direction in a solution of n-butanol: acetic acid: water (6:1:2) for seven hours and in the second dimension in 15% acetic acid. The chromatograms were observed under ultraviolet light both before and after the application of ammonia fumes. The chromatograms were then dipped into a solution of one part 1% potassium ferricyanide and one part 2% ferric chloride, in dilute HCl, and finally in water. The spots were identified by means of the Rf values in two dimensions and color reactions with the treatments described above.

Cytology. Inflorescences were fixed in absolute ethanol: glacial acetic acid: chloroform (9:3:1). After fixation, the material was transferred to 70% ethanol and stored at —15° C. Pollen mother cells were stained with iron-propionic carmine. The pachytene stage, as well as later stages of meiosis, was examined in putative hybrids and in the parental species.

RESULTS

Chromatography. A list of Rf values and color reactions of compounds found in *Petalostemon gattingeri* and *P. purpureum* is given in Table 1. Twelve compounds are specific to *P. purpureum* and six compounds specific to *P. gattingeri.* The chromatographic profile of *P. purpureum* is shown in Figure 1A and that of *P. gattingeri* in Figure 1B. With the exception of one plant, every putative hybrid was found to have some compounds specific to each of the two species. However, no single plant exhibited all of the compounds specific to each species. Table 2 shows the number of plants in which each species-specific compound occurred in each population.

Cytology. Meiosis was found to be completely normal in pollen mother cells of the parental species. The pachytene stage of meiosis is particularly useful for karotype analysis in this genus. Figures 2 and 3 show pachytene cells of *Petalostemon gattingeri* and *P. purpureum,* respectively. The nucleolus and nucleolus organizer are prominent, as well as chromatic and achromatic regions of the seven pairs of chromosomes. No significant differences were found in the karyotypes of the two species (Walker, unpublished).

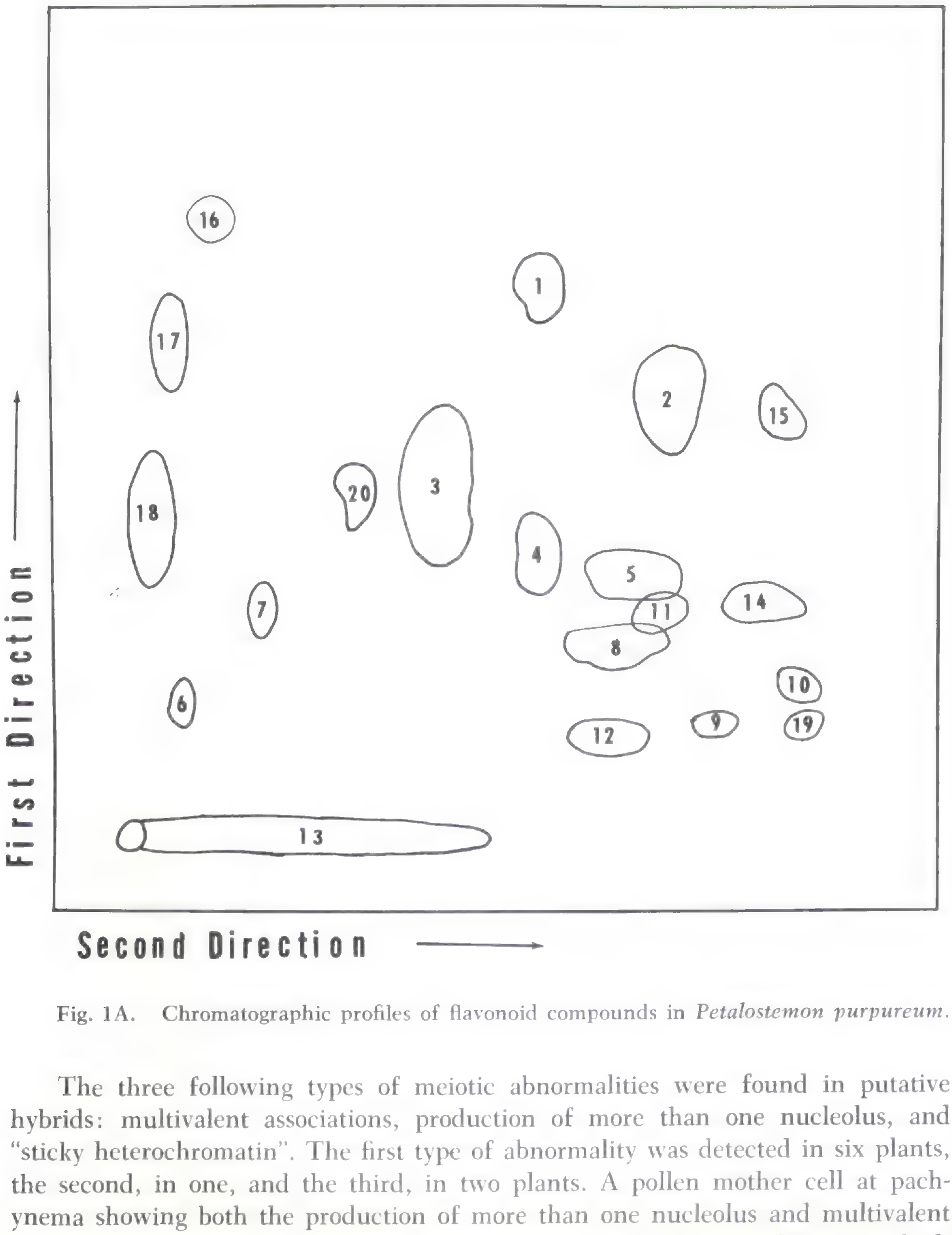

Fig. 1A. Chromatographic profiles of flavonoid compounds in *Petalostemon purpureum*.

The three following types of meiotic abnormalities were found in putative hybrids: multivalent associations, production of more than one nucleolus, and "sticky heterochromatin". The first type of abnormality was detected in six plants, the second, in one, and the third, in two plants. A pollen mother cell at pachynema showing both the production of more than one nucleolus and multivalent associations is shown in Figure 4. "Sticky heterochromatin", a condition in which the heterochromatic regions of several chromosomes are attached to each other, is shown in Figure 5. Completely normal meiosis was found in three of the hybrids shown.

Discussion

Wemple (personal communication) found meiosis to be regular in artificially produced F_1 hybrids between *Petalostemon gattingeri* and *P. purpureum*, indicat-

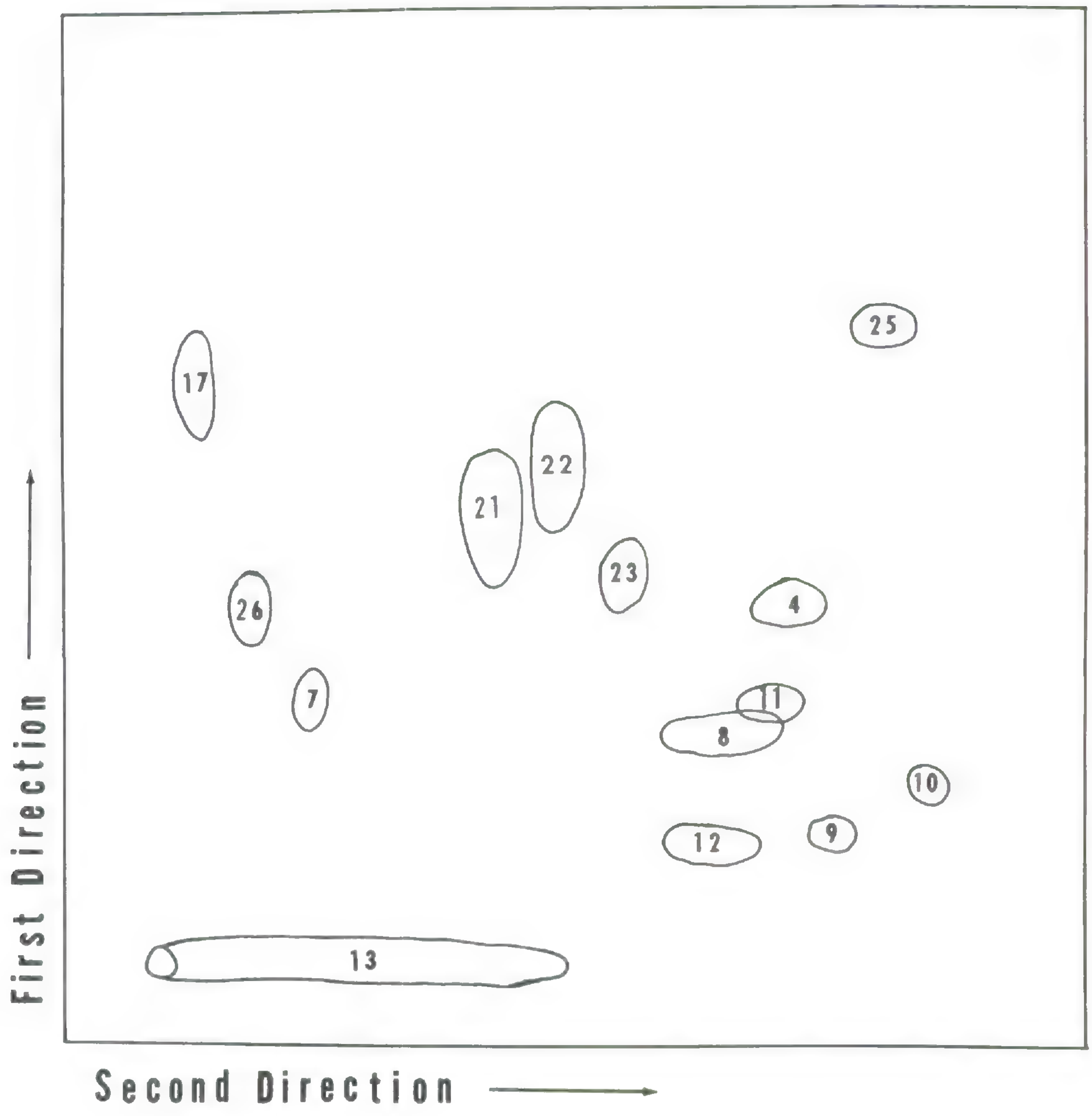

Fig. 1B. Chromatographic profiles of flavonoid compounds in *Petalostemon gattingeri*.

ing that there are no major chromosomal differences between these two species. Karyotype analysis (Walker, unpublished) has also shown no differences in chromosome structure of the parents. The occurrence of multivalent formation in hybrid derivatives is therefore indicative of genic disharmony.

The presence of two nucleoli in hybrid derivatives is also indicative of genic disharmony. Navaschin (1934) showed that in interspecific hybrids of *Crepis*, there is competition among nucleolar organizers. Nucleolar organizers of different species differ in their competitive abilities, and in interspecific hybrids the stronger nucleolar organizer suppresses the weaker one. In hybrids between species which have organizers of about the same strength, both organizers function, and two nucleoli are produced. It seems likely that in *Petalostemon gattingeri* and *P. purpureum*, one of the two nucleolar organizers is normally suppressed but that in

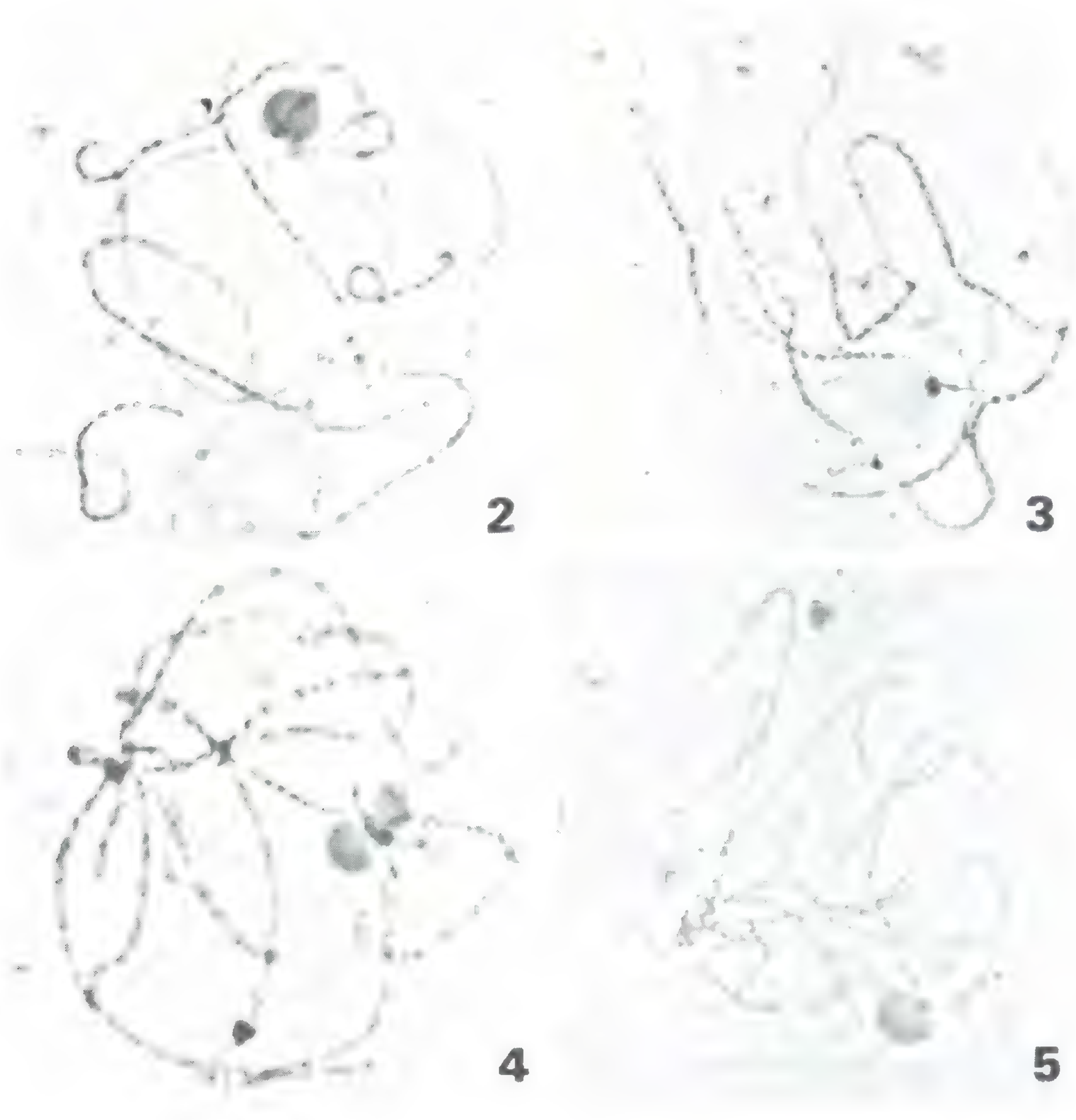

Fig. 2-5. Pachytene stage of meiosis in pollen mother cells. Fig. 2. *Petalostemon gattingeri*, × 868. Fig. 3. *P. purpureum*, × 1073. Fig. 4. Hybrid, × 1195. Fig. 5. Hybrid, × 1200.

some hybrid derivatives this suppression does not occur because of the particular gene combination present.

The third type of abnormality, sticky heterochromatin, may also be the result of genic imbalance. Nielsen (1961) has found this condition in meiotic prophase derivatives of *Agroelymus turneri,* a putative hybrid of *Agropyron dasystachyum* and *Elymus innovatus*. This condition, described by Nielsen as "accumulation of pycnotic materials," produced lethality in the microsporocytes. He concluded that this abnormality may be the result of an unbalanced enzyme and nucleoprotein condition.

Since no structural differences in the chromosomes of *Petalostemon gattingeri* and *P. purpureum* were revealed by karyotype analysis, and since meiosis in the F_1 hybrids is regular, it is concluded that abnormalities in hybrid derivatives of

TABLE 1
COMPOUNDS FOUND IN PARENTAL SPECIES

Spot #	Rf, 1	Rf, 2	UV	UV + NH_3	$FeCl_6$ + $K_3Fe(CN)_6$	P*	G*
1	0.74	0.55	white	—	—	+	—
2	0.59	0.73	light blue	—	—	+	—
3	0.48	0.41	purple	yellow	+	+	—
4	0.39	0.55	purple	yellow	+	+	—
5	0.36	0.69	purple	—	—	+	—
6	0.19	0.07	white	—	—	+	—
7	0.31	0.18	yellow	—	—	+	+
8	0.26	0.66	purple	yellow	—	+	+
9	0.16	0.79	white	—	—	+	+
10	0.21	0.90	white	—	—	+	+
11	0.32	0.72	white	—	+	+	+
12	0.14	0.65	—	—	+	+	+
13	0.02	0.27	pink	—	+	+	+
14	0.33	0.85	—	—	+	+	—
15	0.57	0.88	pink	—	+	+	—
16	0.83	0.10	bright blue	—	—	+	—
17	0.66	0.05	pink	yellow	—	+	+
18	0.45	0.02	light blue	yellow	—	+	—
19	0.11	0.91	white	—	+	+	—
20	0.46	0.30	white	—	—	+	—
21	0.53	0.39	purple	—	+	—	+
22	0.57	0.47	light blue	—	—	—	+
23	0.46	0.55	purple	—	+	—	+
24	0.42	0.74	light blue	—	—	—	+
25	0.74	0.85	—	—	+	—	+
26	0.41	0.11	yellow to pink	—	—	—	+

* P, compound found in *Petalostemon purpureum;* G, compound found in *P. gattingeri.*

TABLE 2
OCCURRENCE OF SPECIES-SPECIFIC COMPOUNDS IN PUTATIVE HYBRID POPULATIONS

	Compound Specific to *P. purpureum*	Specific to *P. gattingeri*	No. of plants in population #1 with compound (total: 10 plants)	No. of plants in population #2 with compound (total: 10 plants)
1.	+	—	6	4
2.	+	—	4	1
3.	+	—	8	8
4.	+	—	5	8
5.	+	—	3	7
6.	+	—	8	10
14.	+	—	3	0
15.	+	—	1	2
16.	+	—	6	9
18.	+	—	6	10
19.	+	—	7	6
20.	+	—	2	4
21.	—	+	5	6
22.	—	+	2	4
23.	—	+	6	6
24.	—	+	5	4
25.	—	+	3	1
26.	—	+	4	2

these two species are the result of genic disharmony and not the result of structural chromosomal differences.

The chromatographic data provide evidence for natural hybridization between these two species and support Wemple's conclusion that barriers to hybridization are ecological and not genetic.

Anderson (1949) has pointed out that the evolutionary role played by introgressive hybridization is the enrichment of variation in the participating species. In considering the significance of hybridization in the two populations studied here, one must take into account that *Petalostemon gattingeri* is much more abundant in these areas than *P. purpureum* since the limestone glade habitat of *P. gattingeri* is more prevalent in the area than is the typical prairie habitat of *P. purpureum*. Therefore it appears that the consequences of introgression will be an increase in the variability of the *P. gattingeri* and a gradual disappearance of *P. purpureum* individuals from the population.

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THE GENUS HOFFMANNIA (RUBIACEAE) IN PANAMA

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ABSTRACT

Eleven new species of *Hoffmannia* (*Rubiaceae*) and diagnoses of nine previously described species from Panama are presented. A key to the species is included.

The tropical genera *Hoffmannia* Sw., *Hamelia* Jacq., and *Bertiera* Aubl. constitute the tribe *Hamelieae* of the *Rubiaceae,* with the first two genera restricted to the tropics of the New World. Paul Standley, in his treatment of *Hoffmannia* in the *North American Flora* (*Rubiales—Rubiaceae* (pars) 32(3): 190-208, 1934), recognized 50 species extending from Mexico to Panama, with two species, *H. pedunculata* Sw. and *H. tubiflora* Griseb. & Desv., occurring in the West Indies. Airy Shaw (in Willis, *A Dictionary of the Flowering Plants and Ferns* ed. 7, Cambridge Univ. Press, 1966) notes that there are 100 species of *Hoffmannia.* Standley, in the *North American Flora* (loc. cit., pp. 191-193), as well as in the *Flora of Costa Rica* (Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1311-1313, 1938) furnishes the only keys to species of *Hoffmannia* published in relatively recent times; these are accompanied by specific diagnoses.

Hoffmannia is a genus of the rain forest with the majority of species occurring at higher altitudes. In Panama, for example, *Hoffmannia* is generally found at altitudes of 3000 to 6000 ft, although a few species may occur at sea level or at low elevations.

Panama seems to represent a good collecting ground for *Hoffmannia* and is rivaled or surpassed in number of species only by Costa Rica and Guatemala. The fact that eleven new species from Panama are described in this paper suggests the need for an intensification in the collecting of the genus, at least in Central America. Prior to 1959 only about 50 collections from Mexico and Central America were to be found in the herbarium of the Missouri Botanical Garden, with the majority of these from the Province of Chiriquí in Panama. Not a solitary collection from the Panamanian Province of Darien was numbered among these. In the last decade about 50 new Panamanian collections have been added to the herbarium. Particularly noteworthy are the 1968 collections of Dr. James Duke and Mr. Joseph Kirkbride, Jr. from the provinces of Bocas del Toro, Chiriquí, and Darien. Currently, *Hoffmannia* is known from seven of the nine provinces of the Republic; thus far the genus has not been collected in the provinces of Herrera and Veraguas.

The genus *Hamelia* seems to be the lowland counterpart of *Hoffmannia.* In Panama *Hamelia* is rarely seen at high elevations, although the author has seen *H. patens* Jacq. in the region of Boquete, Prov. Chiriquí, at approximately 5000 ft elevation. Several characters give evidence of the natural relationship of the two genera: imbricate petals, numerous ovules borne on axile placentas, reticulate

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or foveolate seeds, and raphide-laden fruit walls (as well as other organs of the plants). *Hoffmannia* is obviously more advanced in an evolutionary sense than is *Hamelia:* A number of species of *Hoffmannia* are herbaceous, while *Hamelia* is consistently suffrutescent or arborescent. Such additional features as interspecific variability in floral color in *Hoffmannia,* or the development of tumescences on the petioles of two species (*H. vesciculifera* Standley and *H. kirkbridei* Dwyer) suggest the greater adaptability of *Hoffmannia.*

Vegetative, Floral and Fruit Characters

From approximately 1916 to 1953 Paul Standley published extensively on the systematics of *Hoffmannia.* While he exhibited remarkable ability to recognize novelties in the genus, he all too frequently failed to describe the species in precise fashion. His keys to species are not fundamentally sound, as firstly, he utilized few morphological characters in his couplets, and secondly, some characters (e.g. the length of the calycine teeth or the relative length of the corolla lobes to the corolla tube) used in the leading couplets of the keys are extraordinarily difficult to assess in herbarium material. The fact that he rarely utilizes androecial and gynoecial characters in his keys seems to confirm this criticism.

a. *Vegetative Characters*

The fact that the stipules are rarely observed in *Hoffmannia* even in the field, despite the presence of obvious stipular scars, deprives the taxonomist of a presumably important diagnostic character. Leaf shape and petiole length are the most important foliage characters in *Hoffmannia.* The leaves of the vast majority of species tend to be sparsely hairy; those which appear to be glabrous usually show under magnification a few hairs on the proximal portion of the costa on the lower side of the blade. In texture the leaves range from membranaceous to subcoriaceous and do not tend to be succulent except in *H. davidsoniae* Standley and *H. eliasii* Dwyer. Frequently coarse hairs (?) matted into a crystalline crust are visible under high magnification in *H. kirkbridei.* The occurrence of a few stellate hairs in this same species is noteworthy in view of the fact that Solereder (*Systematische der Dicotyledonen* 501, 1899) and Metcalfe and Chalk (*Anatomy of the Dicotyledons* **1:** 445. Oxford Univ. Press, 1950) consider the *Rubiaceae* to be characterized by unicellular trichomes. Raphides and cystoliths are abundant in the foliage and should be studied in this genus as well as in *Hamelia.* The pigmentation of the leaves of *H. rubripigmenta* Dwyer is noteworthy.

b. *Non-vegetative Characters*

Hoffmannia is characterized by axillary inflorescences, and no exceptions have been noted. Peduncle length, pedicel length, and the relative density of the flowers may be important diagnostic features, although at least one well-collected Panamanian species (*H. pittieri* Standley) shows a disconcerting amount of intraspecific variation. The multiflowered conglomerate inflorescences of *H. areolata* Standley, *H. aeruginosa* Standley, and *H. vesciculifera,* as well as *H. longicalycina* Dwyer simulate those of *Cephaelis,* although those of *Hoffmannia* are simpler as they lack the complex of bracts and bracteoles subtending the flowers of *Cephaelis.*

Bud morphology may be a useful taxonomic character; e.g. the buds of *H. lewisiana* Dwyer are remarkably clavate at the apex, while those of *H. rubripigmenta* are narrowly oblong. The flowers of *Hoffmannia,* as represented by the corolla tube, show a wide range of color interspecifically. Field observations on several species (*H. psychotriaefolia, H. pittieri,* and *H. woodsonii*) indicate that the colors are constant intraspecifically. *Hoffmannia davidsoniae,* on the other hand, seems to have a corolla which varies from yellow to a mixture of yellow and red.

In view of Standley's reluctance to emphasize floral characters in his specific diagnoses, particularly of the androecium and gynoecium, it may be profitable to examine these in detail, at least for the Panamanian representatives. In the case of the hypanthium its shape, ribbing, degree of pubescence, and abundance of raphides are difficult to assess taxonomically. Intraspecific variation in the length of the calycine lobes of *H. longicalycina* Dwyer is obviously diagnostic. No glands were observed alternating with the calycine lobes [as are found e.g. in the Mexican *H. discolor* (Lemaire) Hemsley], except in part of one flower of a collection of *H. pittieri* Standley *(von Hagen & von Hagen 2078).*

The ratio of corolla lobe length to tube length is particularly unsatisfactory as a diagnostic character, the lobes tending to reach full size before the tube completes its elongtaion. The corolla tube is usually glabrous within; externally it may be glabrous or pubescent. The external surface should be examined carefully under magnification as the hairs are frequently very minute.

The stamens offer more important characters than perhaps appreciated by previous workers. The connective of the anthers is produced apically in *H. woodsonii* and basally in *H. fimbrianthera* Dwyer. While the stamens usually number four in *Hoffmannia, H. eliasii* usually has three, and some species occasionally have five stamens, e.g. *H. lewisiana.*

The pistil is usually bicarpellate, although the ovary of *H. psychotriaefolia* may have three or very rarely four locules. The pulvinate ovarian disc is less prominent than in *Hamelia* and is presumably not an important diagnostic feature. The style is elongate, regularly slender, and glabrous. The terminal stigmas are usually connate, may separate naturally at anthesis (e.g. in *H. psychotriaefolia*), or may be teased apart with dissecting needles. In the Panamanian *Hoffmannia* at least three basic shapes characterize the stigmas: club-shaped or clavate connate stigmas (most species), linear or narrowly oblong (e.g. *H. psychotriaefolia, H. areolata*), and lance-shaped (*H. lancistigma* Dwyer). Predictably, stigma morphology will play a major role in establishing sections within the genus when it is monographed.

The fruits of *Hoffmannia* at the terminal stage of maturity are fleshy, although this stage is rarely encountered in collections, possibly because the fruits are soon deciduous in the field. The most widely distributed species, *H. psychotriaefolia,* is usually collected in an immature stage of fruit and can be identified immediately by the fact that the fruit is narrowly oblong and is twice as long as wide. The importance of ribbing in the fruits of *Hoffmannia* is difficult to assess as so few fruiting collections are available for study. The seeds usually show very little variation interspecifically, a circumstance also noted in *Hamelia.*

KEY TO THE PANAMANIAN HOFFMANNIA

a. Petioles vesciculiferous.
  b. Leaf-blades to 25 cm long; petioles to 4 cm long; fruits red .... 19. *H. vesciculifera*
  bb. Leaf-blades to 40 cm long; petioles to 20 cm long; fruits white ... 10. *H. kirkbridei*
aa. Petioles not vesciculiferous, or petioles absent.
  b. Leaves petiolate.
    c. Hairs of hypanthium to 1.7 mm long; inflorescences usually epedunculate and densely capitulate.
      d. Small trees; petioles 0.5-0.8 cm long; stigmas clavate ..... 1. *H. aeruginosa*
      dd. Herbs; petioles 1-4 cm long; stigmas linear-oblong ..... 3. *H. areolata*
    cc. Hairs of hypathium absent or less than 1 mm long; inflorescences usually pedunculate or patulous.
      e. Fruits (immediately before becoming fleshy) at least 2 × longer than wide; stigmas linear-oblong, spreading, ca ⅓ the length of the style ..... 16. *H. psychotriaefolia*
      ee. Fruits less than 2 × longer than wide; stigmas if linear-oblong, very short and not patulous.
        f. Calycine lobes, at least in fruit, to 12 mm long; seeds visible through the wall of the fruit ..... 13. *H. longicalycina*
        ff. Calycine lobes 1-3 mm long; seeds not visible through the wall of the fruit.
          g. Inflorescences rhizomatous; stamens 3 to 4.
            h. Leaves oblong-rotund; flowers yellow to yellow-brown or yellow-red; corolla lobes ca 3 × the length of the corolla tube; anthers 4; stigmas clavate-rotund ..... 6. *H. davidsoniae*
            hh. Leaves oblong or obovate-elliptic; flowers red; corolla lobes less than 2 × the length of the corolla tube; anthers usually 3; stigmas narrowly oblong ..... 7. *H. eliasii*
          gg. Inflorescences not rhizomatous, but axillary in the erect parts of the stem; stamens 4(-5), rarely 6 (often 3 in *H. ostaurea*).
            i. Anthers with the connective not produced apically or basally.
              j. Flowers at maturity ca 2 cm long; calycine lobes 4-5(-6); stamens 4-5; stigmas 3-4; ovaries 3-4-loculate ..... 12. *H. lewisiana*
              jj. Flowers at maturity to 1.5 cm long; calycine lobes regularly 4; stamens 4; stigmas 2-3; ovaries 2-3-loculate.
                k. Lamina of leaf membranaceous; stamens 3(4) ..... 14. *H. ostaurea*
                kk. Lamina of leaf thin-chartaceous to subcoriaceous; stamens 4(-5).
                  l. Stigmas lanceolate ..... 11. *H. lancistigma*
                  ll. Stigmas capitate-rotund to digitiform.
                    m. Leaf blades rubescent, the pigment extractable on boiling; flowers subsessile ..... 17. *H. rubripigmenta*
                    mm. Leaf blades not rubescent, not yielding pigment on boiling; flowers obviously pedicellate.
                      n. Leaves oblong-rotund or widely oblong, exceeding 5 cm in width; calycine teeth to 1.2 mm long.
                        o. Leaves chartaceous to subcoriaceous, not membranaceous and translucent on drying.
                          p. Leaves widely oblong to ovate-subrotund, to 11 cm long, subcoriaceous, the lateral veins 7-9; inflorescences compressed, the flowers few .... 5. *H. cercidifolia*

pp. Leaves elliptic or obovate-elliptic, 9-35 cm long, chartaceous, the lateral veins (11-)15-20; inflorescences usually patulous, the flowers numerous . . 15. *H. pittieri*

oo. Leaves membranaceous and translucent on drying.

q. Leaves to 25 cm long; pedicels 0.5 mm wide; calycine lobes to 1.1 mm long; corolla tube pubescent; stamens 3(-4) . . . . . 14. *H. ostaurea*

qq. Leaves 10-16 cm long; pedicels ca 0.25 mm wide; calycine lobes 0.4-0.8 mm long; corolla tube glabrous; stamens 4 . . . . . 4. *H. capillacea*

nn. Leaves narrowly oblong, usually ca 5 cm wide; calycine teeth 1-2 mm long . . . . . 2. *H. angustifolia*

ii. Anthers with the connective produced apically or basally.

r. Stems cane-like; leaves to 9.5 cm wide; anthers with the connective produced basally; flowers purple . . . . . 8. *H. fimbrianthera*

rr. Stems not cane-like; leaves usually 3 cm wide; anthers with the connective produced apically; flowers yellow . . . . . 20. *H. woodsonii*

bb. Leaves sessile.

s. Leaves rounded toward the apex; calycine lobes 3-4 mm long. . . . . 9. *H. haydenii*

ss. Leaves acute or acuminate toward the apex; calycine lobes less than 1 mm long . . . . . 18. *H. subauriculata*

1. *Hoffmannia aeruginosa* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 1313, 1938.

Shrubs to 4 m, the branchlets slender, terete, the bark pale-brown, ferrugineous-villosulose, the hairs deciduous, leaving a minutely tuberculate surface. *Leaves* with petioles 5-8 mm long, often slightly curved or reflexed, densely ferrugineous-villosulose, to 3 mm wide; blades oblong, shortly acuminate at the apex, widely to narrowly cuneate at the base, to 20 cm long and 8 cm wide, stiffly chartaceous, scarcely discolorous, drying brown or green, minutely foveolate, glandular-shiny, the raphides more conspicuous beneath, moderately abundant, white, divergent, to 0.5 mm long, the costa subplane and slender above, prominulous beneath, minutely ferrugineous to glabrescent, the secondary veins ca 15, arcuate, prominulous, the intervenal areas often appearing lineolate under magnification. *Inflorescences* disposed in uppermost axils, the cymes with 3-10 flowers on peduncles which are reduced to a thickening (or absent), ferrugineous-pubescent or purple-villose, the pedicels absent or the flowers subsessile. *Flowers* with the hypanthium with elongate soft ferrugineous hairs to 1.7 mm long, the calycine teeth subulate, to 1.5 mm long; corolla densely villose on the outside, the lobes acute; stamens with the anthers ca 3 mm long, not produced at apex and base, acute at the apex; ovary 2-loculate, the stigmas ball-shaped. *Fruit* not seen.

COSTA RICA: Zarcero, 1,500 m, *Smith A 86* (F, holotype); Guadalupe de Zarcero, 1,525 m, *Smith H 659* (F, MO).

PANAMA: BOCAS DEL TORO: Fish Creek Mts, vic Chiriquí Lagoon, *von Wedel 2289* (MO).

2. *Hoffmannia angustifolia* Standley, Contr. U.S. Nat. Herb. **20:** 206, 1919.

Distribution: Known to occur from Mexico to Panama.

PANAMA: CHIRIQUI: Quebrada Velo, *Woodson & Schery 261* (F).

The solitary collection cited for Panama appears to belong to this species. As the narrow-leaved species of *Hoffmannia* are so poorly known taxonomically I am hesitant about preparing a detailed diagnosis at this time, although numerous collections of the species exist, especially from Costa Rica. The leaves of *Woodson & Schery 261* are elongate and very narrow, and are attenuate-acuminate at the apex. The linear-oblong buds have calycine lobes which are deltoid and 1-2 mm long; the hypanthium is deeply ribbed; the ovary is 2-loculate; and the stigmas are connate, forming a clavate mass.

3. *Hoffmannia areolata* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 52, 1940.

Herbs to 2 m tall; stems smooth, glabrous or villose. *Leaves* with petioles 1-4 cm long; blade elliptic, attenuate-acuminate at the apex, the acumen to 3 cm long, cuneate at the base, to 25 (?) cm long and 8.5 cm wide, chartaceous, concolorous, the costa immersed above, plano-compressed below, apparently glabrescent above, appressed villosulose on the costa below, distinctly areolate, the raphides numerous, scattered, white, linear, to 0.3 mm long, the secondary veins to 25, arcuate. *Inflorescences* in the uppermost axils of the leaves, sessile, conglomerate, to 2 cm long or longer, often wider than long. *Flowers* with the hypanthium oblong-rotund, covered with elongate ferrugineous hairs to 1.7 mm long, the calycine lobes 4, ca 3.5 mm long, obtuse; corolla ca 4.5 mm long, the tube cylindrical, ca 1 mm wide, the lobes shorter than tube; stamens 4, ovate, ca 1.5 mm long, the connective not produced at apex and at base; ovary 2-loculate, style ca 2.5 mm long; stigmas 2, digitiform, spreading, ca 1.5 mm long. *Fruits* scarlet (fide *Davidson 40*).

PANAMA: CHIRIQUI: Boquete, vic Bajo Choro, 6000 ft, *Davidson 40* (F, holotype; GH, MO isotypes); *Woodson & Schery 661* (F, GH, MO).

The flowers are described as yellow or greenish. This species is marked by having leaves with numerous secondary veins, densely conglomerate inflorescences, and hypanthia with elongate ferrugineous hairs.

4. *Hoffmannia* **capillacea** Dwyer, spec. nov.

Suffrutices, caulibus lignosis laevibus glabris, cicatricibus petiolorum modice conspicuis, nodis hic ca 1 cm distantibus. *Folia* petiolis ad 5 cm longis, ca 0.2 cm latis, leviter alatis, strictis; lamina oblonga, apice subacuta acuminataque, acumine ad 1 cm longo, basi acuta et vix symmetrica, 10-16 cm longa, 5-7 cm lata, membranacea, discolor, supra opaco-viridior, glabra, costa utrinque subcomplanata infra leviter alata, venis lateralibus ca 10, vix prominulis, venis tertiariis

prominulis et patulis. *Inflorescentiae* in axillis superioribus dispositae, glabrae, pedunculo 1-15 mm longo, ca 0.3 mm lato, capillaceo, floribus 2-4 in ramulis patulis saepe subradiate dispositis, pedicellis 6-8 mm longis, capillaceis, ad 0.4 mm longis, ad 0.4 mm latis, glabris. *Flores* (hic in gemmis solum vidi) hypanthio ca 3 mm longo, squarroso, glabro, carnoso, lobis 4, vix conspicuis, acutis, ca 0.4(-1?) mm longis, puberulis; corolla lobis 4, acutis, glabris; stamina 4, antheris ca 2.5-3 mm longis, connectivis apice basique non productis, filamentis brevibus, ca 0.7 mm latis; ovarium 2-loculare, pariete carnoso, stigmatibus oblongo-rotundis, ca 1.5 mm longis, quam stylo latioribus. *Fructus* non visi.

PANAMA: COCLE: Mts N El Valle, 2500-3000 ft, *Lewis, MacBryde, Oliver & Ridgway 1783* (MO, holotype).

This new species is readily distinguished by its membranaceous leaves and delicately capillaceous peduncle and pedicels. The flowers are described as white.

5. *Hoffmannia* **cercidifolia** Dwyer, spec. nov.

Frutices, ramulis gracilibus laevibus glabris. *Folia* petiolis gracilibus, ad 4.5 cm longis, ca 0.15 cm latis; lamina ovato-subrotunda vel lato-oblonga, apice cuneata, acumine falcato vel recto, ad 1 cm longo, ultime subacuto, basi obtusa vel truncata, 7-11 cm longa, 5.5-8 cm lata, in sicco discolor, supra opaco-rubro-fusca, omnino glabrescens (fortasse in costa venisque subtus pilosa) sub lente minute nitido-foveolata, venis lateralibus 7-9, arcuatis, subtus prominulis. *Inflorescentiae* non rhizanthae, ad 1 cm longae, floribus paucis, nutantibus, pedunculo paene nullos, pedicellis brevibus. *Flores* (hic gemmas solum vidi) hypanthio brevi campanulato, costato, glabro, cupula calycis brevi inconspicuaque, dentibus 4, triangularibus, ca 1 mm longis, carnosis glabris; corolla tubo brevi, ca 2.5 mm longo, subcarnoso intus glabro extus pubescenti, lobis 4, oblongis, ca 4 mm longis; stamina 4, antheris ca 3.5 mm longis, ca 0.8 mm diam, connectivis apice basique non productis, filamentis complanatis; ovarium 2-loculare, stylo ca 5.5 mm longo, stigmatibus 2, in capitulum clavato-rotundum dispositis, ovulis multis. *Fructus* non visi.

PANAMA: DARIEN: Cloud forest, Cerro Campamento (S of Cerro Pirre), *Duke 15597* (MO, holotype).

This new species is readily distinguished by its ovate-subrotund leaves with very few lateral veins. The general appearance of the leaves is suggestive of the redbud, *Cercis canadensis* L., so common in much of the United States.

6. *Hoffmannia davidsoniae* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 53, 1946.

Herbs to 1.5 m; stems terete, rigid-carnose, smooth, glabrous, usually drying tan, the internodes to 9 cm apart. *Leaves* with petioles 2-7 cm long, slender and somewhat wiry, 1-2 mm wide, puberulent; lamina oblong-rotund, rounded and acuminate at the apex, the acumen 5-18 mm long, rounded or tapering widely, then abruptly cuneate at the base, 8-17 cm long, 4-12 cm wide, thinly and stiffly succulent, smooth, lustrous, brown, minutely white-puberulent to glabrous above, minutely puberulent on veins beneath, the costa prominulous to subplane above,

prominent below, the principal veins 12-15, widely arcuate, prominulous, 6-12 mm apart. *Inflorescences* mostly rhizomatous, the peduncles elongate, ascending, 5-10 cm long, 1-2 mm wide, rubescent, glabrous, terminated by 3-4 usually radiately disposed patulous branches, the cymules ascending, each branch 7-17 flowered, the pedicels stiff, glabrous, to 5 mm long, ca 0.3 mm wide. *Flowers* with the buds obviously acute at the apex, the hypanthium strongly 6-8-ribbed, emerald-green then red, to 3 mm long, the calycine lobes flaring, deltoid, 0.3-0.5 mm long; corolla to 6 mm long, the lobes 4, much longer than tube, glabrous, the anthers 4, oblong, to 3.8 mm long, the connective not produced at apex or at base, the filaments to 0.6 mm long; ovary 2-loculate, the style to 4 mm long, the stigmas 2, clavate-oblong, ca 1.1 mm wide, each stigma somewhat uncinate. *Fruit* not seen.

PANAMA: CHIRIQUI: Cerro Horqueta, ca 6000 ft, *Blum & Dwyer* 2623 (MO), *Dwyer & Lallathin* 8756 (MO), 8789 (MO); Bajo Chorro, ca 6000 ft, *Davidson* 216 (F, MO, type collection); Bajo Mono & Quebrada Chiquero, 1500 m, *Woodson & Schery* 595 (F, MO).

Like *Hoffmannia eliasii,* this species is succulent and has rhizomatous inflorescences. The corolla is yellow to yellow-brown or yellow above and red at the base. The corolla lobes appear to be almost 3 × the length of the very short corolla tube and in this species represent a reliable diagnostic character (cf. remarks in introduction, p. 5). When the 2 stigmas are pulled apart with dissecting needles they have a claw-like or cheliped appearance.

7. *Hoffmannia* **eliasii** Dwyer, spec. nov.

Herbae ad 1 dm altae, succulentae, caulibus simplicibus basi horizontalibus lignosis, hic 15-20 cm longis, ad 1.2 cm latis, radicibus fibrosis lignosis. *Folia* subsessilia aut plerumque petiolata petiolis ad 12 cm longis, plerumque leviter alatis; lamina oblonga vel obovato-elliptica, apice cuneata ad subobtusa, vix acuminata, basi cuneata ad contracto-cuneata, ad 25 cm longa, ad 9.5 cm lata, rigido-chartacea, vix discolor, glabrescens, ciliis in costa venisque paucis, costa supra prominula, subtus subprominenti ad subplana saepe leviter alata, venis lateralibus principalibus 12-16, leviter arcuatis prominulis plerumque minute alatis, ad 1.8 cm distantibus, venis intermediis irregularibus et mox ramosis tunc evanescentibus, venis tertiariis patulo-pinnatiformibus, vena marginali conspicua, ad 7 mm a margine locata. *Inflorescentiae* rhizanthae, 1-3 cm longae, ad 2 cm latae, pedunculis fortasse 2 per axillam, plerumque strictis, ad 4.5 cm longis, saepe marcescentibus, canaliculatisque pilosis ciliis debilibus diffusisque, pedicellis fere nullis vel ad 4 mm longis. *Flores* hypanthio campanulato in sicco nigro, ca 2 mm longo, glabro, in x-sect costato, dentibus calycinis 4, vix inaequalibus erectis subulatis 1-1.8 mm longis, minute-puberulis; corolla omino glabra, tubo cylindrico, ad 2.5 mm longo, lobis 4, lanceolatis quam tubo longioribus, ad 4.5 mm longis; stamina 3, antheris 3-4 mm longis, subsessilibus, filamentis ca 0.5 mm longis, stylo lineari-cylindrico, connectivis apice basique non productis, stigmatibus 2, inaequali-digitiformibus, ad 0.7 mm longis quam stylo vix latioribus; ovarium 2-loculare. *Fructus* (hic immaturi) pedicellati, pedicellis fortiter adscendentibus,

diffuso-pilosis, ad 4 mm longis, oblongi, ad 0.5 mm longi, ad 2.5 mm lati, calyce persistenti coronati, lobis 1-2.5 mm longis, adscendentibus, in sicco rubri, modice costati, minuto puberuli.

PANAMA: DARIEN: Cana-Cuasi Trail, Chepigna, 4000 ft, *Terry & Terry 1508* (F, GH, MO); Río Cuasi, mainstream, 0-2.5 mi S Tres Bocas, *Kirkbride & Duke 1129* (MO, holotype). SAN BLAS: headwaters Río Mulatupo, *Elias 1779* (MO).

COLOMBIA: CHOCO: Río Nercua, Quebrada Barrial & Quebrada Ambrosio nr Camp Curiche, *Duke 11438* (MO).

Hoffmannia eliasii is named in honor of Dr. Thomas Elias, one of the collectors of the species. It is readily distinguished from its obvious ally *H. davidsoniae*, from the Province of Chiriquí, by its oblong rather than subrotund leaves and much more strict inflorescence. The stamens of the new species are usually three, and the stigmas are narrowly oblong. A Costa Rican collection, *Austin Smith 905* (NY), resembles the new species in leaf shape, but its inflorescences are subsessile.

8. *Hoffmannia* **fimbrianthera** Dwyer, spec. nov.

Suffrutices caulibus laevibus arundinoideis glabris teretibus, internodis ad 15 cm distantibus. *Folia* petiolis gracilibus laxis, ad 7 cm longis, ad 1.2 mm latis, minute arachnoideo-puberulis; lamina oblongo-rotundata, saepe subfalcata, ad apicem cuneata, acumine ad 1.5 cm longo, ad basim acuta vel angusto-cuneata, ad 19 cm longa, ad 9.5 cm lata, papyracea, vix discolor, in sicco grisea, sub lente conspicue foveolata, supra glabrescens, infra in venis solum granuloso-puberula, costa supra plana, subtus vix prominenti, venis lateralibus ca 15, divergenti-arcuatis, subtus conspicue prominulis, venis intermediis patulo-pinnati-formibus, vena marginali undulata a margine ca 8 mm distanti. *Inflorescentiae* sessiles, floribus paucis fortasse (3-)5(-10) subsessilibus vel ad 1 mm longis. *Flores* hypanthio rotundo-oblongo, ca 3 mm longo, sublaeve rigido-carnoso ferrugineo-puberulo, lobis calycinis 4 patulis uncinato-subulatis, ad 1 mm longis, puberulis; corolla carnosa extus ferrugineo-puberula intus minuto-farinosa, lobis fortasse 4; stamina 4, antheris oblongis, ad 3.2 mm longis, minute apiculatis, connectivo basi fimbria patula petaloidea ad 3 mm longo ornato; ovarium 2-loculare, ovulis multis, stylo ad 3.5 mm longo, ad 0.2 mm lato, ad apicem latiore, stigmatibus 2 clavato-connatis, ca 0.35 mm latis. *Fructus* non visi.

PANAMA: BOCAS DEL TORO: Río Teribe just below Puerto Palenque, 350 m, *Kirkbride & Duke 556* (MO, holotype).

This new species is described by the collectors as a "cane-like, coppiced shrub; flowers ramiflorous, tetramerous, purplish." The basal, adaxial, skirt-like protusions of the connective of the stamens and the purple flowers are outstanding features of the species. The same androecial character was noted in some anthers of *H. aeruginosa* Standley, a species not closely related.

9. *Hoffmannia* **haydenii** Dwyer, spec. nov.

Herbae caulibus in vivo fortasse teretibus, in sicco 4-angularibus, glabrae. *Folia* sessilia; lamina obovato-elliptica vel oblonga, versus apicem rotunda, apice acuminata, acumine ad 1.5 cm longo vel fortasse longiore, versus basim contracto-

cuneata, tunc ultime auriculata, auriculis ad 1 cm latis, ad 35 cm longa, ad 14 cm lata, tenui-coriacea, discolor, supra in sicco brunnea, supra glabrescens, subtus in costa venisque puberula, costa supra subplana et leviter canaliculata, subtus vix prominula, ad 3 mm lata, venis lateralibus ca 20 (fortasse pluribus), supra complanatis subtus prominulis. *Inflorescentiae* rhizanthae, 1.5-7 cm longae, pedunculis 1.2-6 cm longis, capillaceis, ca 0.3 mm latis vel 1.3 mm latis, substrictis puberulis in vivo rubris, ad 2.5 mm longis, puberulis. *Flores* gemmis apice cuneato-acutis, hypanthio puberulo vix costato, lobis calycinis 4, erectis lanceolatis, 3-4 mm longis, in sicco purpureo-rubris puberulis; corolla lobis 4, hic ca 5 mm longis, extus puberulis quam tubo longioribus; stamina 4, antheris ca 3.8-4(-5?) mm longis, connectivis apice basique non productis, filamentis brevibus; ovarium 2-loculari, stigmatibus in capitulum clavatum rotundumque aggregatis. *Fructus* non visi.

PANAMA: CHIRIQUI: Finca Collins, ca 5000 ft, *Hayden 117* (MO, holotype).

This new species is obvously related to Standley's *H. subauriculata,* known only from fruiting material collected at Cartago, Costa Rica, which also has leaf-blades that are dilated and clasping. *H. haydeni,* however, has much thicker leaves, longer pedicels, and much more elongate calycine lobes.

10. *Hoffmannia* **kirkbridei** Dwyer, spec. nov.

Suffrutices ad 2 m alti, caulibus teretibus (?) in sicco minuto-rugulosis glabris. *Folia* petiolis ad 13 cm longis, in medio ca 3 mm latis, infra basim laminae conspicue turgidis, inflationibus oblongis, 6-10 cm longis, in sicco ca 1 cm latis; lamina elliptico-oblonga, apice subrotunda ad lato-cuneata, acumine ad 1.5 cm longo, ad 40 cm longa, ad 20 cm lata, rigido-chartacea, in sicco discolor, costa supra prominula canaliculataque subtus subprominenti versus basim distincte suberoso-alata, venis lateralibus 15-25, ad 3 cm distantibus, arcuatis supra vix prominulis, subtus conspicuo-prominulis, venis intermediis plus divergentibus mox evanescentibus, venis tertiariis patulis irregulari-pinnatiformibus, supra fortasse glabra, subtus in costa venisque interdum tegeticulis ciliorum simplicium apresorum crystallinorum ornata, ciliis paucis stellatis. *Inflorescentiae* plerumque 3 per axillam, pedunculis reflexis, 1-1.5 cm longis, ca 1.3 mm latis, tegetibus minutis ciliorum crystallinorum et raphidium instructis, ciliis paucis, ad 0.7 mm longis, rare stellatis, floribus subsessilibus. *Flores* (hic in fructibus juvenilibus partes paucas vidi) hypanthio brevi modice villoso, raphidibus crebris albis, cupula calycis brevi subturgida villosa, dentibus 4, crasso-carnosis (in medio solum?) ciliatis, ad 4.5 mm longis, ad 3.5 mm latis, venis paucis adscendentibus; ovarium 2-loculari, pariete hypanthii crasso, ovulis multis. *Fructus* maturi non visi, seminibus crasso-reticulatis rhomboideis, ca 6 mm diam.

PANAMA: BOCAS DEL TORO: Buena Vista, Almirante, *Cooper* 225 (F); Quebrada Huron, rapid streams through evergreen seasonal forest, ca 300-400 ft, *Kirkbride & Duke* 429 (MO, holotype).

This species is obviously related to the Panamanian *Hoffmannia vesiculifera* Standley, known from the Provinces of Chiriquí and Coclé, the only other species of the genus with vesiculiferous petioles. *Hoffmannia kirkbridei,* named after

Mr. Joseph Kirkbride, Jr., is readily distinguished by its extraordinarily large leaves, perhaps the largest of the genus, which resemble those of *Pentagonia* (*Rubiaceae*). The calycine lobes are unusually large for a *Hoffmannia,* especially in width. The presence of occasional stellate hairs on the leaves of the new species is noteworthy, as stellate hairs have not been reported in *Hoffmannia.*

11. *Hoffmannia* **lancistigma** Dwyer, spec. nov.

Frutices caulibus arundinoideis teretibus et laevibus, ciliis minutis crebris ferrugineo-moniliformibus deciduis. *Folia* valde adscendentia, bene distantia, 2.5-3.5 cm distantia, petiolis ad 7.5 cm longis, ferrugineis; lamina oblonga, apice obtusa, vix acuminata, ultime obtusa, basi cuneata, plerumque asymmetrica, in sicco discolor, papyracea vel rigido-chartacea, sub lente minute granulosa foveolataque, ciliis subtus paucis praeter costam denso-pubescentem, costa supra prominula, subtus prominula, ad 1.5 mm lata, venis secundariis ca 15, arcuatis, subtus prominulis, venis tertiariis patulo-pinnatiformibus. *Inflorescentiae* saepe 1 per axillam, saepe a partibus caulis aphyllis orientes, pedunculo adscendenti, ad 10 cm longo, modice tenui, ca 2 mm lato, substricto vel arcuato, glabrescenti vel sub lente ciliis paucis crystallinis ornato. *Flores* fortasse omnino glabri, hypanthio oblongo, ad 3.8 mm longo, costato, dentibus calycinis 4, erectis triangularibus, ca 1 mm longis, corolla tubo brevi tenui-carnoso, lobis 4(-6), ca 4.5 mm longis, carnosis; stamina 4, antheris ca 3.8 mm longis, ad 1.2 mm latis, connectivis apice basique non productis, filamentis ca 1 mm longis, complanatis, ad 1 mm latis; ovarium 2-loculare, stylo ca 4 mm longo, stigmatibus 2, lanceolatis, ca 2.8 mm longis, ad 0.8 mm latis, crassis quam stylo latioribus in medio constrictis.

PANAMA: CHIRIQUI: Cerro Horqueta, ca 6000 ft, *Dwyer* 7735 (MO, holotype).

As the specific name suggests, this new species is distinguished by its lance-shaped stigmas. A preliminary study of more than 20 Panamanian species of *Hoffmannia* suggests that stigma morphology may well represent one of the most important diagnostic characters in the genus; these fall into three kinds: 1) ball-shaped, resulting from 2 or 3 stigmas being subconnate, 2) linear, and 3) lanceolate.

12. *Hoffmannia* **lewisiana** Dwyer, spec. nov.

Frutex, ramulis laevibus glabris canaliculatis. *Folia* petiolis ad 4.5 cm longis, glabris; lamina oblonga, apice subcontracto-acuta acuminataque, acumine ad 1.5 cm longo, basi acuta et fere symmetrica, concolor, supra glabra, subtus solum in costa venisque puberula, costa supra subplana, canaliculata, subtus prominula, ad 0.15 cm lata, venis lateralibus ± 12, supra planis, subtus prominulis, arcuatis, postremo manifeste patulo-reticulata; stipulae non visae. *Inflorescentiae* ad 6.5 cm longae, ad 4 mm latae, patulae, pedunculo brevi, ramis pluribus, 2-4 cm longis, 0.8-1.8 mm latis, cymis paucis alternatim vel saepe subradiate dispositis, pedicellis 1-7 mm longis, ca 0.4 mm latis, dense albido-puberulis. *Flores* gemmis clavatis (lobis corollae clavate aggregatis sed ultime acutis), hypanthio oblongo, ad 7 mm longo, carnoso, puberulo et conspicue costato, dentibus 4-6, erectis,

cuneatis vel triangularibus, inaequalibus (uno saepe conspicue reducto), ad 2.5 mm longis, puberulis; corolla tubo ad 11 mm longo, carnoso, lobis 5, ad 5.5 mm longis, extus puberulis; stamina 4-5, antheris ca 3.5 mm longis, ca 1.3 mm latis, connectivis apice basique non productis, filamentis complanatis, ca 1 mm latis; ovarium (2-)3-4-loculare, stylo 12-14 mm longo, stigmatibus (2-)3-4, in capitulum rotundum dispositis. *Fructus* non visi.

PANAMA: CHIRIQUI: vic Cerro Punta, 6800 ft, cloud forest and disturbed edge, *Ridgway & Solis 2413* (MO, holotype).

This new species, named in honor of Dr. Walter Lewis of the Missouri Botanical Garden, is readily distinguished by its extraordinarily large flowers, whose perianth parts and stamens are usually in fives, and whose gynoecium is occasionally quadriloculate. As the diagnosis indicates the perianth parts may occasionally be in sixes.

13. *Hoffmannia* **longicalycina** Dwyer, spec. nov.

Suffrutices ramulis laevibus glabris, nodis hic 1 cm distantibus. *Folia* petiolis ad 10 cm longis, angulari ad plano-compressis, ad 2 mm latis, ciliis albis simplicibus, crasso-subulatis tegetes crustaceas formantibus; lamina oblonga, ad apicem cuneata, acumine brevi, ad 1 cm longo, ultime acuto, basi attenuato-cuneata, costa subtus prominula porcataque, ad 2 mm lata, rigido-chartacea, vix discolor, in sicco viridis, supra glabrescens, subtus in costa venisque appresso-ciliata, ciliis interdum rigidis appresso-falcatis albidis, venis lateralibus ca 16, patulo-arcualtis prominulis. *Inflorescentiae* ad 3.5 cm longae, in capitula axillaria floribunda conglomerata dispositae, pedicellis ad 3 mm longis, puberulis. *Flores* non visi. *Fructus* oblongi, in x-sect teretes, hic ad 12 mm longi, ca 7 mm lati, extus leviter costati, pubescentes ciliis aliquibus ad 2 mm longis ferrugineis debilibusque, lobis calycinis persistentibus 5, erectis lineari-lanceolatis, ad 12 mm longis, ca 2 mm latis, petaloideis pubescentibusque, 2-loculares, seminibus multis crasso-reticulatis, ca 0.5 mm diam, per parietem tenuem visibilibus.

PANAMA: DARIEN: Cana-Cuasí Trail betw Cerro Campiamento & La Escalera to "paramo" E of Tres Bocas, *Kirkbride & Duke 1278* (MO, holotype).

This new species is distinguished from all other species of *Hoffmannia* by the length of the calycine lobes. The elongate calyx suggests the genus *Amphidaysa* Standley, with three species in the New World tropics. *Hoffmannia longicalycina,* however, has a complete septum, at least in the basal part of the fruit, and two locules, and has the reticulate seeds characteristic of *Hoffmannia.* The seeds are visible through the thin wall of the dried fruit, a character which I have not hitherto observed in the many *Hoffmannia* fruits examined.

14. *Hoffmannia* **ostaurea** Dwyer, spec. nov.

Suffrutices succulenti, ramulis in sicco canaliculatis, glabrescentibus, sub lente areabus ciliorum aggregato-crustaceorum ornatis, ramulis juvenilibus crebris raphidibus notatis, internodis 1.5-3 cm distantibus. *Folia* petiolis arcuato-ascendentibus, ad 8 cm longis, in sicco 2-15 cm latis, glabris, raphidibus crebris; lamina elliptica, apice cuneata brevi-acuminata acumine ad 1 cm longo, basi subcontracto vel lato-

cuneata, ad 25 cm longa, ad 7.5 cm lata, tenui-membranacea, concolor, glabra sed raphidibus vermiformibus ad 0.3 mm longis ornatis, costa utrinque complanata, venis lateralibus 12-15, patulo-arcuatis gracillissimis, venis tertiariis irregulari-pinnatiformibus, areabus reticulatis conspicue patulis. *Flores* (hic gemmas solum vidi) glabri, hypanthio oblongo-rotundo, ca 2 mm longo, non costato, lobis calycinis 4 inaequalibus subulatis, ad 1.2 mm longis, raphidibus crebris albidis; corolla subcarnosa lobis fortasse 4; stamina 3(-4), antheris ad 3 mm longis, connectivis apice basique non productis, filamentis brevibus; ovarium 2-loculare, stigmatibus 2 in capitulum rotundum ca 1 mm longum dispositis. *Fructus* rotundi, ad 5 mm diam, in vivo rubri, in sicco rubro-purpurei, pedicellis gracilibus, ad 5 mm longis.

PANAMA: BOCAS DEL TORO: Río Teribie below Quebrada Huron & Quebrada Schlunjik, *Kirkbride & Duke 501* (MO, holotype).

The specific latin name *ostaurea* means "mouth of the bull" and suggests the provincial name "Bocas del Toro." This new species is marked by extraordinarily thin leaves; in the dried state these are so translucent that one can read newsprint through them. The axillary inflorescences are very reduced and few-flowered, the latter borne on very slender ligneous pedicels. The fruit at maturity is a striking purple-red color.

15. *Hoffmannia pittieri* Standley, Contr. U.S. Nat. Herb. **18:** 140, 1916.
Hoffmannia panamensis Standley, Contr. U.S. Nat. Herb. **20:** 204, 1919.

Shrubs to 8 m tall, the thicker branches smooth, drying tan, terete, glabrous, hollow in the center. *Leaves* with petioles 5.5-7 cm long, 1.5-3 mm wide, the lamina often slightly decurrent, elliptic or obovate-elliptic, acute to cuneate, or rarely subrotund at the apex, acuminate, the acumen to 2 cm long, acute to attenuate-cuneate at the base, 9-35 cm long, 8-12 cm wide, the larger blades 2.5-3 × longer than wide, chartaceous, usually slightly discolorous, usually drying tan or brown, glabrous, the costa prominulous above, prominulous to prominent beneath, often ligneous, to 2.5 mm wide, the lateral veins (11-)15-20, widely arcuate, 1(-2.2) cm apart, with 1-2 conspicuous irregular veins between each pair of laterals. *Inflorescences* in the uppermost axils, patulous, 3-9 cm long, the primary peduncle compressed as a nodal pad, or elongate, the secondary peduncles 1-4 glabrous, the flowers usually patulous, the pedicels to 15 mm long, stiff, glabrous. *Flowers* with the hypanthium carnose, ribbed, sparsely puberulent to glabrous, the calycine teeth 4, deltoid, 0.6-2 mm long; corolla to 13.5 mm long, subcarnose, glabrous to sparsely puberulent, the lobes 4(-5), 2.3-4.3 mm long, 1.7-3 mm wide; stamens 4, the anthers 2.3-4.5 mm long, the connectives not produced at apex and at base, the filaments to 1.8 mm long; ovary 2-4-loculate, the style to 11 mm long, the stigmas usually ball-shaped, 1.2-1.8 mm long, wider than style, each stigma ovate-oblong to cordate. *Fruits* subrotund, the calycine lobes persistent, to 6.5 mm long, glabrous, drying red-brown, scarcely ribbed, the seeds brown, foveolate.

Distribution: Known only from the higher elevations of Chiriquí and neighboring Bocas del Toro.

Panama: bocas del toro: Robaldo Trail, N slopes Cerro Horqueta, *Allen 4962* (MO). chiriquí: Cerro Punta, 2000 m, *Allen 1533* (MO); Boquete, Finca Collins, ca 5000 ft, *Dwyer & Hayden 7654* (GH, K, MO, UC, US), *7665* (F, GH, K, MO, NY, UC, US), *Stern et al. 1127* (MO); El Boquete, Bajo Chorro, *Davidson 47* (F, MO), *51* (F, MO); Boquete, Cerro Horqueta, *Blum & Dwyer 2599* (MO), *2643* (MO), *2647* (MO), *Duke et al. 13651* (MO), *Dwyer 7654* (MO), *Dwyer & Hayden 7745* (GH, MO), *Dwyer & Lallathin 8756* (MO), *8783* (MO), *8790* (MO), *Kirkbride 147* (MO), *von Hagen & von Hagen 2076* (F, NY), *2078* (NY); betw Pinola & Quebrada Hondo to summit on Chiriquí Trail, *Kirkbride & Duke 894* (MO); Upper Valley Río Chiriquí Viejo, vic Monte Lirio, 1300-1900 m, *Seibert 165* (F, NY, MO); Río Chiriquí Viejo, *White & White 2* (F, NY, MO), *74* (F, GH, MO); vic Casita Alta, Volcán de Chiriquí, 1500-2000 m, *Woodson et al. 839* (F, MO, NY).

Virtually all of the collections cited above were made at or very close to Cerro Horqueta in the Province of Chiriquí, the type locality of the species. *H. pittieri* is the tallest of the Panamanian *Hoffmannia* species, reaching up to 25 ft in height. It is distinguished from the other species of the Republic by its hollow stem (older branches), large leaves with numerous lateral veins, and large flowers usually born on elongate pedicels. The inflorescence is very variable as to the structure of the peduncles. Noteworthy is the fact that the pedicel length in the fruits does not appear to be correlated with the length of the floral pedicels, the latter being longer in the material examined. The flowers are orange-yellow (those of *Davidson 51* are described as "whitish green"), and the fruit is red at maturity.

16. *Hoffmannia psychotriaefolia* (Benth.) Griseb., Fl. Brit. W. Ind. 321, 1861.

Higginsia psychotriaefolia Benth. in Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn **1852**: 50, 1852.

Shrubs to 2.5 m tall, the stems ultimately slender, terete, glabrous, rubescent. *Leaves* with petioles to 9 cm long and 2 mm wide; lamina oblong, acute and finally attenuate-acuminate at the apex, the acumen to 2.5 cm long, acute and inequilateral at the base, to 20 cm long and 8 cm wide, usually 3-4 × longer than wide, stiffly chartaceous, concolorous or discolorous, glabrescent, usually with minute, scattered, white granulations on both surfaces, the lateral veins 10-12, widely arcuate. *Inflorescences* in the axils of the uppermost leaves, the peduncles reduced to a pad or to 8 mm long, the flowers radiately disposed, to 7 per inflorescence, the pedicels slender, to 4 mm long. *Flowers* to 12 mm long, the hypanthium 2-4 mm long, scarcely ribbed, often with abundant red raphides, the calycine teeth 4, cuneate-deltoid, 0.8-2 mm long, acute; corolla 8-11 mm long, the lobes 4, thickly petaloid, often longer than the tube at maturity; stamens 4, the anthers 2-2.8(-4) mm long, the connective not produced at apex and base, the filaments ca 0.5-1 mm long; ovary 2-3-loculate, the style to 5.5 mm long; stigmas 2, linear, equal, spreading at maturity, 2-3.3 mm long. *Fruits* with pedicels radiately disposed, slender, shorter than the pericarp, oblong to ovate-oblong, obtuse or truncate at apex, to 8 mm long, at least 2 × longer than wide, at first delicately ribbed, smooth, glabrous, often drying yellow, finally fleshy, china-red, pink, or purple.

Distribution: Guatemala to Panama.

PANAMA: CHIRIQUI: vic "New Switzerland", central valley, Río Chiriquí Viejo, *Allen 1329* (F, MO); Boquete, *Ebinger 671* (MO); Bajo Chorro, 6000 ft, *Davidson 198* (MO); Finca Collins, *Dwyer & Hayden 7666* (MO), *7681* (GH, MO, US), *Hayden 162* (MO), *Kirkbride 120* (MO); Cerro Horqueta, *Dwyer et al. 518* (GH, K, MO, NY, UC, US), *Dwyer & Hayden 7653* (GH, US), *7664* (GH, K, MO, UC, US), *von Hagen & von Hagen 2054* (F, NY), *2174* (NY); Palo Alto, E Boquete, 5000 ft, *Stern et al. 1015* (MO); Quebrada Velo, 1800 m, *Woodson & Schery 258* (F, MO); Bajo Mono & Quebrada Chiquero, *Woodson & Schery 564* (F, MO); Casita Alta, Volcán de Chiriquí, *Woodson et al. 884* (MO, NY). COCLE: betw Cerro Pilón & El Valle de Antón, 700-900 m, *Duke & Dwyer 13972* (MO).

Hoffmannia psychotriaefolia is readily distinguished in the fruiting stage, at least prior to a terminal period of fleshiness, as the fruits are at least twice as long as wide, a condition not observed in Panamanian species or in many extra-Panama sheets examined in various herbaria. In the flowering stage it is often confused with *H. woodsonii,* but it is distinguished from the latter by its much larger leaf-blades with more lateral veins. The flowers are yellow, and the fruits vary from pink to red, presumably being a china-red as they approach maturity.

17. *Hoffmannia* **rubripigmenta** Dwyer, spec. nov.

Herbae lignosae, humiles, ramulis glabris raphidibus crebris minutis oblongis ornatis. *Folia* petiolis ad 1 cm longis, leviter alatis; lamina obovato-elliptica, apice late cuneata, ultime obtusa, versus basim contracto-cuneata et vix decurrens, ad 23 cm longa, ad 9.5 cm lata, chartacea, in sicco opaco-rubra, fortasse glabra, costa utrimque prominula, venis lateralibus ca 8, arcuatis, venis intermediis plus divergentibus, tunc ramosis et evanescentibus; stipulae non visae. *Inflorescentiae* petiolo quam paullum longiores, pedunculo gracili, erecto, glabro, ad 2 cm longo, ca 5 mm lato, in sicco rubro, floribus ca 8, subsessilibus. *Flores* (hic gemmas solum vidi) gemmis angusto-oblongis, ca 1 mm latis, hypanthio oblongo, ad 2.5 mm longo, carnoso, glabro, ecostato, dentibus calycinis erectis cuneatis acutis, ca 1.5 mm longis, vix connatis, corolla carnosa, tubo fortasse brevi, lobis 4, glabris; stamina 4, antheris ca 4 mm longis, connectivis apice basique non productis; ovarium 2-loculare, pariete hypanthii crasso ad 3.5 mm lato, stylo cylindrico, stigmatibus erectis digitiformibus, ca 1.3 mm longis, vix quam stylo crassioribus. *Fructus* non visi.

PANAMA: DARIEN: upper Río Membrillo & Camp 7 on Construction Rd to San Blas, 100-800 m, *Duke 10870* (MO, holotype).

On boiling the flowers and the leaves one extracts a red pigment. I have not encountered this in any other species of the genus studied. The buds are very narrow and the digitiform stigmas suggest a possible relationship with *H. psychotriaefolia.* The flowers are described as pinkish.

18. *Hoffmannia subauriculata* Standley, Jour. Wash. Acad. Sci. **18:** 179, 1928.

Herbs, short, woody, the roots fibrous, the stems strongly quadrangular to terete, smooth, glabrous. *Leaves* sessile, the blade elliptic to obovate-elliptic, or obovate-spatulate, acute and short-acuminate at the apex, cuneate and often widely so at the base, to 2.5 cm wide at the base, ultimately obtuse or vaguely auriculate, 9-30 cm long, 5-10 cm wide, stiffly chartaceous, glabrous with ∞

linear raphides, the costa porcate above, prominent beneath, the lateral veins 10-25, widely arcuate, prominent beneath, usually 1.5-2.5 cm apart, with usually a conspicuous intermediate vein between a pair of principal veins. *Inflorescences* with the peduncle arising at or near the ground line, the peduncles wiry but not stiffly erect, here to 4 cm long, the cymules few-flowered. *Flowers* (only buds seen) with the hypanthium glabrous, the calycine teeth 4, cuneate-subulate, acute, puberulent, less than 1 mm long; stamens and petals not seen; ovary 2-locular. *Fruits* oblong, here to ca 6 mm long, 4-ribbed, the seeds ca 1 mm long, coarsely foveolate.

Distribution: Known from one collection at Cartago, Costa Rica, and from Bocas del Toro and Darien, Panama.

PANAMA: BOCAS DEL TORO: s. loc., *von Wedel 361* (MO). DARIEN: Cerro Pirre, *Bristan 627* (MO).

Standley, in his description of the type, states that the leaves are membranaceous; those of the Panamanian collections are stiffly chartaceous. The flowers of *von Wedel 361* are described as white, and those of *Bristan 627* as lilac.

19. *Hoffmannia vesciculifera* Standley, Publ. Field Columbian Mus., Bot. Ser. **4:** 285, 1929.

Shrubs, presumably densely ferrugineous and arachnoid flocculose. *Leaves* with petioles to 4.5 cm long, conspicuously inflated for most of their length, the inflations to 1 cm wide, located nearer the blade than the node, densely ferrugineous-flocculose; leaf-blades oblong-rotund to obovate-oblong, briefly acuminate at the apex, cuneate to rounded at the base, to 25 cm long and 15 cm wide, chartaceous, discolorous, drying brown, usually foveolate above, the hairs diffuse, to 5 mm long, often calcareous at base, confined to veins and venules, the costa immersed above, prominulous to plano-compressed beneath, the principal secondary veins 12-25, widely arcuate to substrict, the margin often weakly ciliolate. *Inflorescences* to 5 cm long, the peduncles to 2 cm long, the flowers numerous in densely bracteate axillary capitula, these rounded or compressed-rotund, the pedicels to 4 mm long, glabrous; bracts linear-lanceolate, to 1.5 cm long, 0.3-1.5 mm wide, with 1-2 irregular ascending submarginal veins, the margins glandular-pectinate-ciliate, the hairs to 4 mm long. *Flowers* with the hypanthium oblong, truncate apically, glabrous, delicately 4-ribbed, the calycine lobes 4, unequal in length and width, lanceolate, tapering narrowly above middle, 7.5-10 mm long, 1.5-2 mm wide, the hairs ferrugineous, marginal, to 2 mm long, usually densely aggregated above middle; corolla with lobes shorter than tube; stamens 4, the anthers with connective not produced at apex or at base; ovary 2-locular, the style slender, the stigmas clavate, spreading at maturity, wider than and ca ¼ length of style. *Fruits* oblong-rotund, here to 5 mm long and 4.5 mm wide, delicately-ribbed, the ribs ca 10, the pericarp thin-walled, the raphides abundant, the hairs deciduous, the calycine lobes 4, persistent, linear-lanceolate, to 10 mm long, the hairs deciduous in patches, the seeds mostly rectangular to cuneate, coarsely reticulate.

PANAMA: BOCAS DEL TORO: Chiriquí-Calderas Trail betw Higueron & Gutiorrea, *Kirkbride & Duke 761* (MO); E slope La Zorra to divide, mossy forest, cloud forest, *Kirkbride & Duke 829* (MO); Water Valley, vic Chiriquí Lagoon, *von Wedel 1514* (F, MO); Fish Creek Mts, vic Chiriquí Lagoon, *von Wedel 2284* (MO). COCLE: Cerro Caracoral, elfin forest, *Kirkbride 1117* (MO).

This is perhaps the easiest of the Panamanian *Hoffmannia* to recognize because of the elongate hairs of the inflorescence and the inflated bases of the petioles which resemble those of *Tococa* Aubl. (*Melastomaceae*). *Kirkbride & Duke 761* note the absence of ants on the swollen petioles. They also describe the stipules as "horny." The inflorescence of *H. vesciculifera* is red, the hypanthium pink, and the corollas yellow. The mature fruits are described as red.

20. *Hoffmannia woodsonii* Standley, Ann. Missouri Bot. Gard. **28:** 471, 1941.

Shrubs 2-3 m tall, the stems glabrous, smooth, the raphides dot-like, white. *Leaves* with petioles 2-6 cm long, to 0.8 mm wide; lamina oblong, attenuate-acuminate at the apex, the acumen to 1 cm long, attenuate-cuneate or acute at the base, 5-12 cm long, 1-5(-6) cm wide, membranaceous or thin-chartaceous, the raphides scattered, white, linear on lower surface, subgranular above, to 0.4 mm long, the costa plano-compressed beneath, the lateral veins 4-8, prominulous (especially beneath), glabrous or occasionally puberulent. *Inflorescences* 1-2 per axil, to 1.5 cm long, compressed, the peduncles reduced to a pad or to 6 mm long, ca 0.5 mm wide, glabrous to ferrugineous-puberulent, the flowers usually 2-6 per cymule, the pedicels 5-7 mm long, often radiately disposed or deflexed-candelabraform, capillaceous, glabrous to ferrugineous-puberulent. *Flowers* with the hypanthium squarrose in x-sect, subcarnose, glabrous or puberulent, the calycine teeth 4(-5), cuneate-subulate, 0.5-1.3 mm long; corolla 7-8 mm long, the lobes 4, ca 4 mm long, delicately carnose, diffusely puberulent on the outside, often delicately-ribbed; stamens 4, the anthers partly exserted at anthesis, 3-4.7 mm long, the connective produced at the apex, then usually ovate-cuneate, to 1 mm long; ovary 2-locellate, the style 4-5.5 mm long, the stigmas 2, oblong-capitate, 1-1.2 mm long, wider than the style. *Fruits* (here not seen in fleshy mature stage) oblong-subrotund, truncate, to 4.5 mm long, the calycine lobes persistent, glabrous, delicately ribbed, the ribs well-spaced, varying in prominence.

Known only from Panama.

PANAMA: BOCAS DEL TORO: betw Gullierrez Quebrada & E slope La Zorra, headwaters Río Mali, Chiriquí Trail, *Kirkbride & Duke 715* (MO). CANAL ZONE: Barro Colorado I, *Croat 5118* (MO). CHIRIQUI: Cerro Horqueta, *Blum & Dwyer 2619* (MO), *Duke et al. 13634* (MO); betw Pinola & Quebrada Hondo toward summit Chiriquí Trail, *Kirkbride & Duke 915* (MO); Boquete, Finca Collins, *Stern et al. 1149* (MO); upper Río Chiriquí Viejo, 1300-1900 m, *White & White 6* (MO), *26* (MO); Quebrada Velo, 1800 m, *Woodson & Schery 260* (F); vic Callejón Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 503* (holotype, F; isotype, MO). COCLE: Cerro Pilón & El Valle de Antón, 700-900 m, *Duke & Dwyer 13972* (MO); Cerro Gaital Caracoral, 2700-3000 ft, *Dwyer & Correa 8910* (MO); Cerro Pilón nr La Mesa, ca 2700 ft, *Dwyer & Lallathin 8593* (MO), *8627* (MO), *8659* (MO), *8681* (MO), *Lallathin 5090* (MO); mts N El Valle de Antón, 2500-3000 ft, *Lewis et al. 1732* (G, MO, US), *Stimson 5033* (MO). LOS SANTOS: Loma Prieta, 800-900 m, *Duke 11849* (MO); Loma Prieta, Cerro Grande, 2400-2800 ft, *Lewis et al. 2212* (GH, MO, US), *2242* (GH, MO, US). DARIEN: s. loc., *Bristan 103* (MO).

This species is often difficult to distinguish from *H. pittieri* and *H. psychotriaefolia*. Its leaf blades are usually much smaller; *Croat 5118*, probably the sole collection of the species made near sea level and the only collection of the genus from the Canal Zone, has larger and wider leaves. The consistently produced apex of connective of the anthers, visible under magnification, readily distinguishes *H. woodsonii* from the two aforementioned species. Its clavate-rotund stigmas readily separate it from *H. psychotriaefolia,* and its smaller leaves with few lateral veins serve to distinguish it from *H. pittieri*.

Excluded Species

1. *Hoffmannia discolor* (Lemaire) Hemsley (Biol. Centr. Am. **2**: 36. 1881) probably does not occur in Panama. One collection, *Terry & Terry 1508* (MO) from Boquete, Prov. Chiriquí, Panama, has been erroneously assigned to this species. It does not have the minute calycine glands and linear anthers which Standley in the North Am. Flora (loc. cit., p. 32) includes in his floral description.

2. Three collections of *von Wedel* [2363 (MO), 717 (F), and 963 (F)] from Chiriquí Lagoon, Prov. Bocas del Toro, probably represent a new species. As these collections belong to the complex of *Hoffmannia* marked by narrow leaf-blades with attenuate-acuminate apices and elongate petioles, a complex in need of critical study on a New World basis, I have elected not to prepare a diagnosis of it.

NOTES

THE SKUNK CABBAGE IN MISSOURI

A single specimen of *Symplocarpus foetidus* (L.) Nutt. has flowered and vegetatively flourished in Jefferson County, Missouri during the spring seasons of 1967-9; whether it has borne fruit during the summers of 1967 and 1968, I do not know. However, the appearance of Skunk Cabbage in Missouri is, so far as I have been able to determine, new: its range is described by Fernald in *Gray's Manual* (8th ed.) as "Que. to se. Man., s. to w. N.S., N.E., L.I., Va., upland to Ga. and Tenn., W. Va., O., Ind., centr. Ill. and Ia." It is not mentioned in Steyermarks' *Flora of Missouri.* Jones and Fuller, in *Vascular Plants of Illinois,* report its most westerly appearance in that state a good deal to the north of us (Henderson County), its closest approach in our approximate latitude in Jasper County. Specimens in the Missouri Botanical Garden Herbarium, dated 1903 and 1907, with notations that they were collected at the Garden by John H. Kellogg, can be presumed to be material from plants cultivated on the Garden premises by Mr. Kellogg.

This leaves us, then, with two anomalies: the first, did the single plant observed to be growing so happily in Missouri arrive there by natural means? It is growing in what is, admittedly, an unnatural—or artificially prepared—habitat: a bog created by walling in the bank of a stream just below a flowing spring. This is on the estate of Jay G. Rice, approximately 8 miles south of Antonia, Missouri, where Charles M. Rice built the wall and did introduce a number of plants before his death. However, Mr. Charles Rice died in 1950 and, to the best of my knowledge, the Skunk Cabbage did not appear for 17 years therafter; I am also entirely sure that no plants have been introduced since 1950.

The second anomaly is the question of why the plant has not spread, even within the boggy area in which the single specimen is growing. The flowers are bisexual, and although proterogynous, Trelease reported (Amer. Nat., Sept 1879, p. 580) that, after the stigmas of the lower flowers have matured, "some can evidently be fertilized by the mere falling of pollen from the upper flowers without any extraneous aid, for pollen is shed in such quantities that it covers the bottom of the spathe." Trelease's classic work on the pollination of this plant was carried on at Cornell, long before he came to Missouri — if the Skunk Cabbage is now following in his footsteps, its pace is a very slow one.—*Erna R. Eisendrath, Missouri Botanical Garden, St. Louis.*

Ann. Missouri Bot. Gard. **56**(2): 287-291, 1969.

SUPPLEMENTARY NOTES ON THE PHYTOLACCACEAE, I.

A study of material at the British Museum and Kew Gardens has yielded a new species of *Lophiocarpus* and the recognition of *Phytolacca polyandra* Batalin.

Lophiocarpus **latifolia** Nowicke, sp. nov.

Herba annua vel perennis, glabra. *Folia* lanceolata-elliptica, ad 10 cm longa et 1 cm lata.—Fig. 1.

Herbs, sparsely branched, slightly suffrutescent at the base, glabrous, to 1 m. *Leaves* lanceolate-elliptic, acute, entire, to 4 cm long and 1 cm wide, calcium oxalate crystals present; sessile or with petioles 2-3 mm long. *Inflorescences* spikes, up to 20 cm long, the larger terminal, the smaller axillary, flowers in clusters of 2-3. *Flowers* perfect, ± actinomorphic, yellow-green; the central flower subtended by a single bract, ca 1.8-2 mm long, weakly 3-lobed, the central lobe much elongate, the 2 lateral flowers subtended by a single bract ca 1.2 mm long and 2 bracteoles ca 0.8 mm long; sepals 5, ± equal, oblong and rounded, ca 2-2.5 mm long and 1-1.6 mm wide, thin, membranaceous; stamens 4, 3 alternate and one opposite, exserted, the filaments ca 2.2-2.5 mm long, the anthers at least 3x longer than broad, ca 0.8 mm long; ovary spherical, 1-carpellate (?), style absent, stigmas 4, thready, ca 1 mm long. *Fruit* an achene, ± globose, ca 1.8 mm long, weakly 8-ridged and ± muricate; seed one, the testa shiny black, the embryo large.

Holotype: Mozambique: lourenco marques: .Bela Vista, betw Tenonganine and Floresta de Licuati, 12 Sept 1961, *Lemos & Balsinhas* 263 (BM).

Pollen grains single, subprolate, ca 23-24μ (E) × ca 28-29μ (P) 3-colpate, colpi ca 17μ long, exine ca 2-2.5μ in thickness, ca 3μ at the poles, sexine ± equal to the nexine and finely reticulated.

Pollen examined: *Lemos & Balsinhas* 263 (BM).

Known only from the type collection, *L. latifolia* can be readily distinguished by its leaves which have a conspicuous blade in marked contrast to the remaining species of the genus, all of which have filiform or linear leaves.

Phytolacca polyandra Batalin, Acta Horti Petropol. **13:** 99, 1893. (Syntypes: *Potanin s.n., Beresowski s.n.* both LE)

P. clavigera W. W. Smith, Bot. Mag. **149:** *pl.* 8978, 1923.

Herbs, coarse and very robust, to 2 m. *Leaves* ovate to elliptic, acute to mucronate, entire, the bases obtuse to attenuate, to 32 cm long and 13 cm wide, ± glabrous, the veins slightly scabrous; sessile or with petioles ca 3 cm long. *Inflorescences* racemes, stout, up to 30 cm long, densely flowered, mostly axillary. *Flowers* with pedicels ca 5-11 mm long, ± winged at the base; bract single, ca 2 mm long, lanceolate; bracteoles two, ca 1 mm long, lanceolate; sepals 5, ovate-elliptic, ca 3-3.5 mm long and 2-2.5 mm wide; stamens 12-16, arranged in 2 irregular whorls, the filaments ca 2.5 mm long, awl-shaped, the anthers ca 1 mm; ovary of 7-9 carpels, ± completely united or with apices slightly free,

Fig. 1. Photograph of holotype of *Lophiocarpus latifolia* Nowicke.

the styles as many as the carpels, ca 1 mm long, the stigma on the upper surface. *Fruit* a berry, ca 7-9 ribbed, ca 7-10 mm in diam, seeds 7-9, each ca 4 mm long, the testa shiny black.

Specimens examined.

CHINA: Kansu, *Beresowski s.n.* (LE); *Potanin s.n.* (LE); SW Szechuan, Mts betw Litang and Shou-Chu Rivers, betw Wa-Erh-Dje and Garu, *Rock 16738* (GH).

Cultivated specimens from Kew Gardens (type of *Phytolacca clavigera* W. W. Smith). Grown from seeds sent by Forrest from Yunnan, China (K).

In an earlier paper on the *Phytolaccaceae* (Nowicke, Ann. Missouri Bot. Gard. **55:** 294-364, 1968) I omitted treatment of this species because of insufficient material to establish its validity. Even at a first consideration, its distinguishing characters, coarse, robust growth form and geographical location of China, appear as unsound bases for specific recognition, the more so in a genus which is noted for its plasticity. However, no other taxon in *Phytolacca* even approximates the growth form and dense inflorescences of *P. polyandra* except *P. acinosa* Roxb. which is easily distinguished by its separate carpels.—*Joan W. Nowicke, Missouri Botanical Garden, and Department of Botany, Washington University, St. Louis.*

KALLSTROEMIA (ZYGOPHYLLACEAE) IN MISSOURI

In his monumental *Flora of Missouri* (Iowa St. Univ. Press, Ames, 1963, p. 966), Steyermark lists the Missouri taxon of *Kallstroemia* Scop. as *K. hirsutissima* Vail. *Kallstroemia intermedia* Rydb. is given as a synonym. Steyermark discusses these two concepts, indicating that some authors maintain them as separate species.

During my studies on *Kallstroemia* [The genus *Kallstroemia* (Zygophyllaceae). Contr. Gray Herb., in press], I have found that, indeed, there is a single taxon of the genus in the state, but that the correct name to be applied to it is *Kallstroemia parviflora* Norton. *Kallstroemia intermedia* is a synonym of *K. parviflora,* while *K. hirsutissima* is a species of the Chihuahuan Desert of the southwestern United States and adjacent Mexico. *Kallstroemia parviflora* is a species of the semiarid grasslands of the Southwest, introduced into Missouri along railroad rights-of-way.

The following collections have been seen from the state:

JACKSON CO.: Courtney, rare along railroad, *Bush 767* (MO); Kansas City, waste ground, *Bush 8168* (GH, MO, NY, US), *8168A* (CAS); Sheffield, *Bush 7281* (GH, MO, NY). ST. LOUIS CO.: Allenton, *Letterman s.n.*, 1897 (MO); Meramec Highlands, *Drushel 5273* (MO). ST. LOUIS CITY: on railroads, *Eggert s.n.*, 1882 (NY), railroads, banks, *Eggert s.n., 1883* (NY).

Steyermark also maps *Kallstroemia* as occurring in Jasper, Jefferson, and Lawrence counties.—*Duncan M. Porter, Missouri Botanical Garden, St. Louis.*

H. L. Chakravarty, who published *Lagenaria bicornuta* as a new species in this journal (Ann. Missouri Bot. Gard. 55: 69. [Sept.] 1968.), had previously published *Lagenaria bicornata* [*sic*] (Bull. Inst. Fondam. Afrique Noire, Sér. A, Sci. Nat. 30: 412. [April] 1968.) based on the same type.—*Editor.*

Erratum: Ann. Missouri Bot. Gard. 55: 398, line 22. For "ca 1.5 longis" read "ca 1.5 mm longis."

The 1969 Jesse M. Greenman Award was presented to Clifford M. Wetmore for his "Lichens of the Black Hills of South Dakota and Wyoming" (Publ. Mus. Michigan State Univ., Biol. Ser. 3(4): 209-464. 1967 [1968].).

The Greenman Award is given by the Alumni Association of the Missouri Botanical Garden for the best Ph.D. dissertation in plant systematics published during the previous year. The award honors Jesse M. Greenman, Curator of the Herbarium from 1919 to 1943. Papers published in 1969 are now being considered and may be submitted until 1 May 1970. Papers may be sent to David M. Gates, Director, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis, Missouri 63110.—*Editor.*

Edgar Anderson, who was associated with the Garden for over 45 years, died suddenly of a heart attack on 18 June 1969.—*Editor.*

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 56, No. 1, pp. 1-112, was published on October 13, 1969.

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VOLUME 56
1969
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ANNALS OF THE
Missouri Botanical Garden

CONTENTS

Tropical Island Biogeography: The Missouri Botanical Garden's Sixteenth Annual Systematics Symposium *Duncan M. Porter* 293
Seasonal Flowering Behavior in Central Panama *Thomas B. Croat* . . . 295
Studies in Neotropical Paleobotany. I. The Oligocene Communities of Puerto Rico *Alan Graham & David M. Jarzen* 308
Wood Anatomy of Goodeniaceae and the Problem of Insular Woodiness *Sherwin Carlquist* 358
The California Islands *Robert F. Thorne* 391
Distribution Patterns of West Indian Mosses *Marshall R. Crosby* . . . 409
Drosophilidae of Hawaii *Hampton L. Carson* 417
Vegetation of a Galápagos Island before and after an Ice Age *Paul A. Colinvaux* 419
Pollen Morphology of Saprophytic Taxa in the Gentianaceae *Siwert Nilsson & John Skvarla* 420
Cytotaxonomic Notes on Some Neotropical Gentianaceae *Richard E. Weaver, Jr.* 439
Spores of the Heterophyllous *Selaginellae* of Mexico and Central America *Robert Lee Hellwig* 444
The Ozark Flora—Some Collections of Note *W. G. D'Arcy* 465
NOTES
Additional Type Material of *Bouvardia* (Rubiaceae) *Will H. Blackwell, Jr. & Marshall C. Johnston* 468
A New Species of *Scaevola* (Goodeniaceae) from Tahiti *Sherwin Carlquist* 469
Chromosome Numbers of Phanerogams. 3. 471
Some new combinations in *Protium* (Burseraceae) *Duncan M. Porter* 475

VOLUME 56
1969
NUMBER 3

ANNALS OF THE
Missouri Botanical Garden

The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden and the Department of Biology of Washington University. Papers originating outside the Garden or University will also be accepted. For information on preparation of manuscripts, see the inside back cover.

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TROPICAL ISLAND BIOGEOGRAPHY: THE MISSOURI BOTANICAL GARDEN'S SIXTEENTH ANNUAL SYSTEMATICS SYMPOSIUM[1]

DUNCAN M. PORTER[2]

MacArthur and Wilson (1967: 3) have stated, "The study of insular biogeography has contributed a major part of evolutionary theory and much of its clearest documentation. An island is certainly an intrinsically appealing study object. It is simpler than a continent or an ocean, a visibly discrete object that can be labelled with a name and its resident populations identified thereby. In the science of biogeography, the island is the first unit that the mind can pick out and begin to comprehend. By studying clusters of islands, biologists view a simpler microcosm of the seemingly infinite complexity of a continental and oceanic biogeography. Islands offer an additional advantage in being more numerous than continents and oceans. By their very multiplicity, and variation in shape, size, degree of isolation, and ecology, islands provide the necessary replications in natural 'experiments' by which evolutionary hypotheses can be tested." Tropical islands were chosen as the subject of the Sixteenth Annual Systematics Symposium in part because of the above reasons. In addition man, as he continues to interfere with his environment, is rapidly decimating many tropical organisms (Porter, 1970), especially those on islands, where native species are less able to compete with disturbed conditions than are introduced weedy species.

The Symposium was held in the Museum building of the Missouri Botanical Garden on Friday and Saturday, 17–18 October 1969. About 215 botanical and zoological systematists, representing 62 institutions in the United States and Canada, attended.

Six papers were presented at the Symposium, with the resulting discussion being directed by the Symposium moderator, Dr. Marston Bates, University of Michigan. Speakers and their topics were Dr. Hampton L. Carson, Washington University, "Drosophilidae of Hawaii"; Dr. Paul A. Colinvaux, Ohio State University, "Vegetation of a Galápagos Island before and after an ice age"; Dr. Thomas B. Croat, Missouri Botanical Garden, "Seasonality in the flora of Barro Colorado

[1] The Symposium was supported by NSF Grant GB-14722.
[2] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Island, Panama"; Dr. Marshall R. Crosby, Missouri Botanical Garden, "Distribution patterns of West Indian Cryptograms"; Dr. Alan Graham, Kent State University, "Tertiary phytogeography of Puerto Rico"; and Dr. Terrell H. Hamilton, University of Texas, "Adaptive radiation and the control of avian endemism in the Galápagos Archipelago." In addition Dr. Sherwin Carlquist, Rancho Santa Ana Botanic Garden, presented an evening talk on "Evolution in the Hawaiian Islands" at Rebstock Hall, Washington University.

The papers given by Dr. Croat, Dr. Crosby, and Dr. Graham, plus the abstracts of the papers by Dr. Carson and Dr. Colinvaux follow in this issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The papers of Dr. Carlquist and Dr. Thorne are the result of discussions which took place during the Symposium.

The Symposium is structured so that a maximum amount of time is available for discussion following presentation of the papers. The discussion periods were particularly rewarding, as they not only provided an opportunity for members of the audience to question the speakers, but also for them to review pertinent aspects of their own research. This situation encouraged a lively exchange of ideas and data, as investigators and their graduate students actively participated in the formal discussions. Both these discussions and the informal conversations that took place outside the formal meetings proved valuable to the participants.

The stimulating papers presented by the speakers, the direction of the discussions by Dr. Bates, and Dr. Carlquist's colorful evening talk all combined to produce a successful Symposium.

LITERATURE CITED

MACARTHUR, R. H. & E. O. WILSON. 1967. The Theory of Island Biogeography. Princeton.

PORTER, D. M. 1970. The rape of Panama. Missouri Bot. Gard. Bull. 53(1): 11–17.

SEASONAL FLOWERING BEHAVIOR IN CENTRAL PANAMA

THOMAS B. CROAT[1]

ABSTRACT

Based upon data obtained from study of herbarium material as well as from field observations on Barro Colorado Island, species are enumerated according to seasonal flowering and fruiting times. Nearly the same number of species flower or fruit during the dry season months as in the wet season. The total number of species in flower or fruit in any one month varies considerably with flowering peaks occurring in February, July, and December. The December peak in flowering is caused largely by trees and vines and to some extent by shrubs and small trees. The July peak is caused by the flowering of both shrubs and small trees as well as herbs. The beginning of the rainy season is a period of maximum vegetative competition, and few species use this period for initiation of flowering.

An understanding of the seasonal fluctuations of plants is essential to our study of ecology and evolution in the tropics. In an attempt to better understand the seasonal pattern of flowering and to establish the sequence of flowering for each species occurring on Barro Colorado Island, I have made a tabulation of seasonal records based on herbarium specimens. The data was obtained from studies made at the Field Museum, Chicago, and the Missouri Botanical Garden and is based on collections made in central Panama with heavy emphasis on Barro Colorado Island. This study of herbarium material follows eight months of observations on the island. Though this report is a preliminary one, the picture of seasonal patterns of flowering represented in central Panama is believed to be reasonably accurate.

Barro Colorado Island, with an area of six square miles, is about three miles in greatest diameter. The island was formed by the damming of the Chagres River which resulted in the formation of Gatún Lake, a principal part of the Panama Canal route. It is centrally located in the Canal Zone about midway between the Pacific and the Caribbean. The topography of Barro Colorado Island consists of a mass of hills, the largest of which is 450 feet above the level of the lake or about 537 feet above sea level. The steep undulating terrain is traversed by over 20 miles of trails which make nearly all of the island accessible. However, since the trees are in general quite tall and the canopy closed for much of the year, collecting plants in the forest can be rather fruitless without the aid of climbing equipment.

The island's approximately 25 miles of shoreline is very irregular and has undergone drastic changes since its formation. The northern and eastern sides of the island undergo considerable erosion on account of wakes produced by ships and strengthened by trade winds. Many of the coves have silted in so that during the dry season, when the level of Gatún Lake drops several feet, the deposits become tongues of land which are invaded by a number of weedy species. This is particularly true of the more protected coves on the southern side of the island. It is here also, in the quiet waters of the southern and western edges of the

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[1] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 56: 295–307. 1969.

island, that several aquatic associations of plants occur most frequently. These associations form the early stages of a hydrarch succession important in building the shoreline. Perhaps the most important of these is the *Acrosticum-Annona glabra* association.

Although no major disturbances of the island's flora or fauna have taken place since 1923, when the island was set aside as a biological preserve, a major portion of the island was cutover 60–70 years ago. This cutting included much of the eastern third of the island, major promontories of the northern side of the island (including Orchid Island), and small portions of the western periphery. Most of the rest of the island is considered by some authorities to be covered with primeval forest. While I doubt this, it is nonetheless very old.

The vegetation is thus primarily advanced secondary to nearly primary forest. It could perhaps be best referred to as semi-evergreen moist tropical forest. The island is rich in plant species — I have recorded 103 species of vascular cryptogams and 1181 species of phanerogams. Dennis Knight, University of Wyoming, who has been making successional studies on the flora for the past several years, reports (personal communication) that even in what appears to be the most homogeneous areas of the island, the species-area curve for trees with greater than 1 inch dbh does not level off in as much as 1.5 hectares (about 3.7 acres). He reports that there are in such areas about 50–60 species of trees per acre.

The island receives about 107 inches of rain in an average year, most of this falling between May and December (Fig. 1). Thus the climate is seasonal with a pronounced dry season beginning sometime in December and extending through January to April. Rains gradually build up to reach a peak in November. With the exception of wind and rainfall, other facets of the physical environment are remarkably invariable particularly at the forest floor. For example Allee (1926) reports that the total variation of monthly mean temperature during the year is only 1.5° F.

The decrease in rainfall during the dry season is reflected in a marked increase in leaf fall. During the mid to late dry season, before leaves are re-initiated, the forest, with leaf litter piling up to a considerable depth on the floor, takes on a much different appearance than during the rainy season. This openness, coupled with the higher wind intensities of the dry season, have a beneficial effect on those species whose fruits are adapted for wind dispersal. This will be discussed later.

Despite the many objections which may be raised, the use of the herbarium for studying seasonality of flowering and fruiting will remain an important tool in our understanding of phenology. This is particularly true for species which are either so rare or so obscure that firsthand observation of their seasonality is very limited. Lowland tropical rain forests have many such species. It is only after the accumulation of many specimens that a composite picture of the seasonality of such species may emerge. Even this picture would be tentative, and only on the scene observation of many representatives of a species over a long period would present a definitive picture.

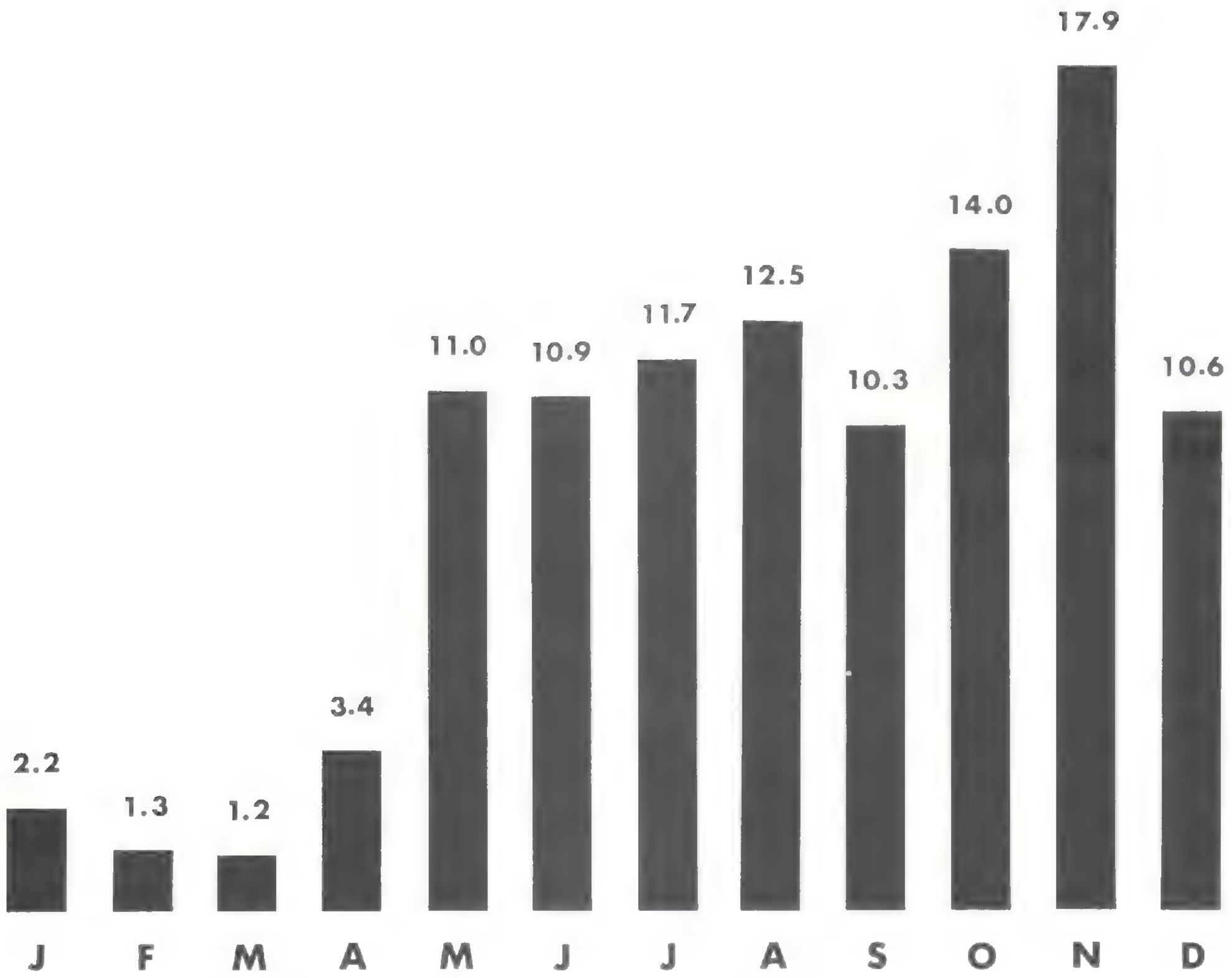

FIGURE 1.—Monthly rainfall, in inches, on Barro Colorado Island. Based on 39 year data from the Meteorological and Hydrographic Branch, Panama Canal Company.

One of the foremost requirements in using herbarium specimens for coming to conclusions concerning phenology is an adequate knowledge of the species involved. Identification of herbarium material is often clearly not to be trusted. It is also helpful to know the species from field experience. Knowledge of the appearance of the fruit at maturity, how the seeds are distributed, and how long a fruit of mature size persists on the plant are all important in evaluating herbarium specimens. There are many species which have fruits collected all year but none of which are mature. Mature fruits are frequently not represented on herbarium specimens because they have fallen or been eaten or because of their size or soft nature.

Even observation of some species in the field can be confusing. Species of *Apeiba* (Tiliaceae), for example, often have fruits on the tree for a full year, yet fruits with viable seeds are quickly removed by monkeys. Old fruits left on the trees by the monkeys probably contain no viable seeds. In the case of *Luehea* (Tiliaceae) and a number of other species the valves of the fruit persist for some time after the seeds have been dispersed with little change in appearance.

A chief disadvantage of using herbarium collections for seasonality studies is that the range of flowering time may be exaggerated, because a species may flower

Seasonality Types	Dry Season J F M A	Wet Season M J J A S O N D	Species in flower less than 9 mos.	Peaks for species in flower more than 9 mos.	Total
1. Flower and fruit dry season			85	54	139
2. Flower and fruit dry-wet			58	48	106
3. Flower and fruit wet			74	59	133
4. Flower and fruit wet-dry			51	59	110
5. Flower dry; fruit dry-wet			31	8	39
6. Flower dry; fruit wet			27	5	32
7. Flower dry-wet; fruit wet			53	8	61
8. Flower dry-wet; fruit wet-dry			17	15	32
9. Flower dry-wet; fruit dry			1		1
10. Flower dry; fruit dry one year late			7		7
11. Flower dry-wet; fruit dry-wet one year later			3		3
12. Flower wet; fruit wet-dry			27	4	31
13. Flower wet; fruit dry			35	14	49
14. Flower wet; fruit dry-wet			8		8
15. Flower wet-dry; fruit dry			22	1	23
16. Flower wet-dry; fruit dry-wet			19	20	39
17. Flower bimodally			22	27	49
18. Flower and fruit continuously without peak				158	158
19. Seasonality unknown					161
		Total	540	480	1181

Table 1. Flowering and fruiting seasons of the plants of Barro Colorado Island. Flowering (———) and fruiting (– –) spans are generalized for the dry (shaded) and wet (unshaded) seasons. The number of species in each seasonality type is given at the right.

abnormally early in one year and abnormally late in another year. On the other hand, the peak flowering period can be accurately determined in the herbarium, provided enough collections are available.

In originally attempting to categorize the seasons of flowering on Barro Colorado Island no more than a half dozen patterns were envisioned. It was found that the patterns are much more numerous and quite complex. In order to avoid competition, plants have altered their flowering periods to fill every possible niche. Species can be grouped into what I feel are 18 meaningful groups of biological importance.

Table 1 depicts the seasonality types. The solid line indicates flowering period and the intermittent line indicates fruiting period. The lines indicate the general spans of the various seasonality types and are not meant to depict any particular species. Thus, for example while all the species in season type 1 both flower and fruit within the dry season, they need not all have flowers and fruits simultaneously. In many season groups several kinds of flowering patterns may be found. Individuals of some species have a progressive development of their flowers and have small fruits which develop quickly. Thus they have flowers and fruits simultaneously throughout much of their flowering period. Good examples of such flowering behavior are found among members of the Gramineae, Cyperaceae, Musaceae, Marantaceae, Polygonaceae, Amarantaceae, Euphorbiaceae, Labiatae, Acanthaceae, and Compositae.

More commonly individuals have distinct flowering and fruiting periods. Maturation of fruit for most species (even those with small fruits) usually occurs after most flowering has ceased. Species with large fruits usually require considerable time for fruit maturation. Consequently the time of flowering and the time of fruit maturation of any individual plant may be separated by a long period of time.

Though perhaps most true of species having small or medium fruits, the staggered onset of flowering of different individuals insures that both flowers and fruits are present on a population of plants for a considerable part of their flowering season. As a result the flowering season of a species is usually much longer than the flowering season of any individual of that species.

Many species are found in flower or fruit over a relatively long period of time. There are 480 such species, about 41% of all phanerogams, which are in flower for more than nine months of the year. These species generally have a definite peak of flowering and fruiting at some time during the year. It is quite possible that the large number of species flowering for nine months or more is merely a reflection of the total range of variation in flowering time as exhibited by specimens collected over a period of many years. Some of these species may be found to flower less than nine months in any given year.

Being unable to decide which phenomenon was of more importance, the seasonal peak or the duration of flowering, those species in flower for greater than nine months were grouped into different classes as seen in the second column of figures of Table 1. For many purposes I concluded that the peak of a species' season was the optimum period of flowering for that species and thus that this peak should be used to classify the species. In many cases the peaks were quite

pronounced with an insignificant number of individuals flowering or fruiting at other times of the year. Thus for this purpose, most of the original set of 18 flowering and fruiting patterns were duplicated for those species flowering more than during nine months. To the right is the total of both of these columns.

From this data I had hoped to come to some conclusion as to which season was more important from the standpoint of species reproduction. The largest single category, disregarding the 161 species for which too little is known to establish seasonality, is the "non-seasonal" group—those species which flower and fruit continuously all year with no obvious peak.

Other large groups are those of species which flower and fruit in the dry season (85 species) or which have their peak of flowers and fruits in the dry season (54 species). The comparable groups for the wet season are very similar and the total number of species is almost identical (139 *versus* 133).

There are 49 species which are either strongly bimodal or which I suspect to be bimodal in their flowering pattern. Of these 27 flower more than nine months. While it is by no means easy to categorize the bimodal species, most of them flower once during the dry season (mostly mid dry season), then flower again sometime in the wet season (usually mid to late wet season). Another tendency for many of the bimodal species is for one burst of flowering to be smaller than the other. *Chrysophyllum panamense* (Sapotaceae) is a good example. Although verifying field work is required, *Chrysophyllum panamense*, on the basis of herbarium material, appears to have a few flowers from January through March and a few fruits six months later in July and August. Many flowers are produced from July through September and many fruits six months later during January through March. The period from April through June shows negligible herbarium material with none seen for October through December.

In the case of *Hirtella triandra* and particularly *H. racemosa* there may be trimodal flowering. Although this might be difficult to detect in the field, herbarium material shows three strong equidistant clusters of fruiting specimens of *H. racemosa*. *Hirtella triandra* shows similar tendencies though not so strong. These species have been included with the bimodal species.

Much more important than I would have originally thought are the "transition" species—those which utilize more than one season for either flowering or fruiting. There are a total of 375 species which flower through such transitional periods, either dry to wet season or wet to dry season. There are 368 species which fruit in a similar manner. These figures are higher than for those species whose flowers or fruits are restricted to either the dry or wet season or for those which peak in either the dry or wet. In other words, there are more transition species than there are restricted species. Perhaps the transition species take advantage of the benefits of both seasons—the openness of the dry season and the moisture of the wet season.

While no attempt has been made to define the actual triggering mechanisms for flowering, there can be little doubt that the onset of the dry season acts in some manner to synchronize flowering of a large percentage of the island's flora. Except for a small peak of flowering activity by some species during July, a month

well within the confines of the wet season, all major components of the vegetation have their major flowering activity sometime during the dry season. In all probability flowering activity of species making up these peaks is due to a reaction to conditions of drought.

In an attempt to establish a composite picture of seasonality a graph (Fig. 2A) has been prepared of the total number of species collected in flower and in fruit for every month of the year. The fact that the fruiting specimens are less frequently collected than flowering specimens is reflected in their almost consistently lower values as depicted on the graphs. A species need have been collected only once to be reported for a particular month. The assumption is made that most species have been collected at least once during most of the months they are in flower or fruit. Although irregular collecting opens the possibility that more initial collections (i.e. species collected for the first time for a particular month) will be made at a particular period of time, it does not seriously affect the data. If one were attempting to establish the peak of flowering of a particular species based upon the total number of specimens, the effect would be a more serious one.

Three major peaks of both flowering and fruiting activity, namely July, December and February, are seen in the graph for all species collected in flower per month (Fig. 2A). There is no significant difference in the peaks of flowering and fruiting except when fruiting drops off in November and flowering increases. If the species flowering per month are separated according to type of habit (Fig. 3), the three points of maximum flowering or fruiting as seen on the composite graph are seen to be caused by different components of the vegetation.

Since differences in seasonal flowering of monocotyledonous and dicotyledonous herbs appear to be insignificant (Fig. 2B) all herbaceous plants are included together for purposes of comparison with other types of habit. Though most of the palms have been excluded from the more typical herbaceous plants, the herbs remain a diverse group of plants. They include annual, perennial, and suffruticose species which may be erect, sprawling, vinelike, epiphytic, hemi-epiphytic, parasitic, or aquatic. Included also are the palmettos and giant monocotyledonous herbs

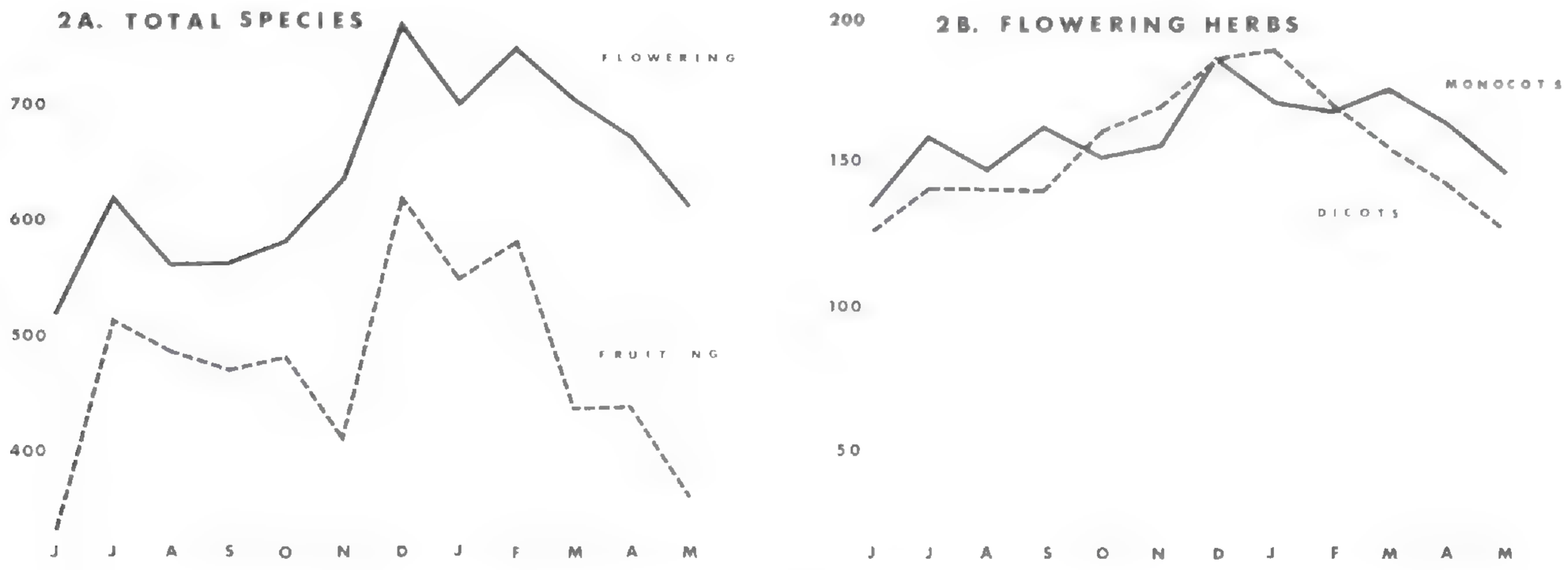

FIGURE 2.—Seasonality of the flora in central Panama.—A. Total number of species flowering (————) and fruiting (– – –) per month.—B. Number of monocot (————) and dicot (– – –) herbs flowering per month.

such as *Musa, Heliconia, Costus* and *Calathea* which may compete with shrubs for light.

Much of the herbaceous element of the vegetation exists in man-made clearings and at the margin of the lake, but a sizeable number of species can be found in the forest. While herbaceous hemi-epiphytes reach the lower levels of the canopy, the true epiphytes as well as a few herbaceous vines may be found in the upper level of the canopy. Most terrestrial herbaceous species in the forest are found along trails and in tree-fall areas where the light intensity is greater.

Because the large and medium-sized trees are subject to similar environmental conditions they have been included together (Fig. 3B). Some of the taller species of palms have been included with this arboreal canopy group. Small trees are not subject to the same environmental conditions as the canopy-level trees and were found to follow a seasonal pattern quite similar to that of the shrubs. Consequently these woody sub-canopy elements of the vegetation were included together (Fig. 3C) for comparison with the canopy-level trees (Fig. 3B), herbaceous plants (Fig. 3A), and woody vines (Fig. 3D).

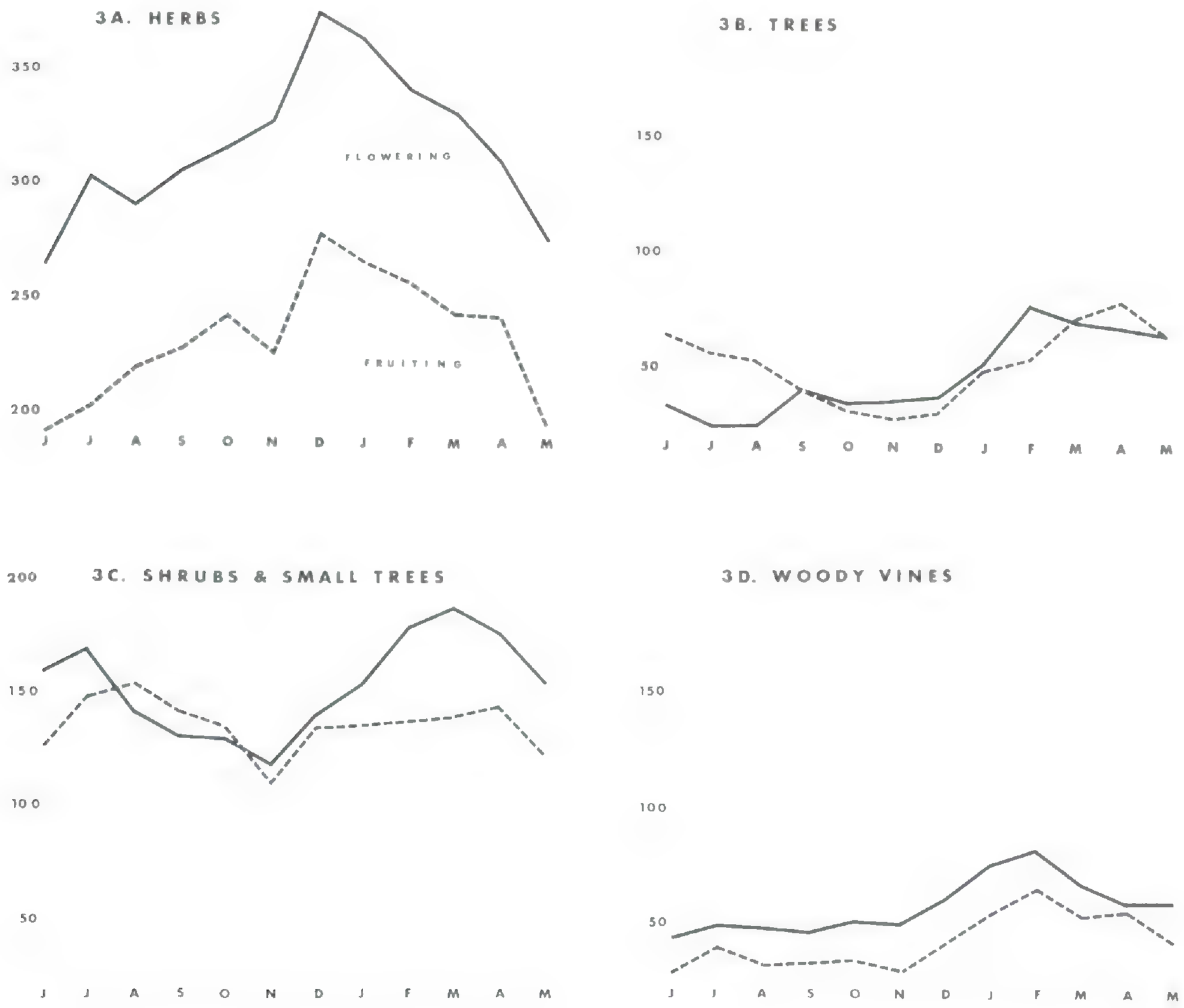

FIGURE 3.—Number of species of various habits flowering (——) and fruiting (– – –) per month in central Panama.—A. Total herbs.—B. Total medium-sized and large trees.—C. Total small trees and shrubs.—D. Total woody vines.

The last component of the vegetation separated for purposes of comparison is the woody vines (Fig. 3D). Most woody vines are found growing above the canopy, but some may hang down to near the ground in clearings or near the edge of the lake. They are easily confused with scandent shrubs which usually do not reach the canopy. This group would be expected to react to seasonal changes in much the same manner as the canopy trees.

Common to all components of the vegetation which are illustrated (Fig. 3) is a low or near low point of flowering activity in June. The July peak found in the composite graph (Fig. 2A) is caused by shrubs and small trees (Fig. 3C) as well as the herbs (Fig. 3A). Flowering of large and medium-sized trees (Fig. 3B) is at the lowest point at this time. This is an indication that the July peak in flowering is a biological phenomenon, possibly a delayed response to the beginning of the rainy season rather than an artificial peak caused by summer collectors. If an inordinate amount of collecting were the cause, one would expect an increase in the number of flowering tree species collected in July as well.

It is not surprising that there is a burst of flowering in July. Species flowering in May are principally dry season species which may extend their flowering into the early rainy season. Few species begin to flower in May, since May and June are months of maximum growth following the beginning of the rains. Maximum growth is essential at this time in order that plants may obtain a favorable position with regard to their competitors. Since competition for light is quite extreme, any plant flowering at this time would be likely to delay its vegetative growth which might be hazardous for its survival. It is possible that by July vegetative competition has become equilibrated and that sufficient food has become available for a resumption of flowering. Of 101 species known to begin flowering in the early part of the rainy season (May–July) only 23 commence flowering in May, while there are 43 which begin flowering in June and 35 in July.

Perhaps more important than May and June from the standpoint of vegetative competition are the latter weeks of April, when rains often begin to fall in greater abundance. While still a dry season month, April receives about three times as much rainfall on the average as does March. Only eight species are known which begin their flowering in April. This is a possible indication of acute vegetative competition at the very onset of the wet season.

Of the 43 species which begin flowering in June only a few expend much energy on the production of flowers. Most are trees, shrubs or vines with a few small flowers. Some are aquatic, riparian, and deep-shade plants for which water is not a critical factor in competition. Epiphytic or hemi-epiphytic plants of usually limited size also number among those species flowering in June.

Herbs. The herbaceous element of the vegetation continues to flourish throughout the wet season following the small July peak and achieves maximum number of species in flower in December (Fig. 3A). This flush of flowering at the beginning of the dry season reflects the ability (also the need) of the herbaceous plants to respond most quickly to changes in the environment. The large number of herbaceous species with a peak of flowering in December may be due in part

to the fact that this month probably contains both rainy season and dry season species.

Because many herbaceous species produce flowers and fruits simultaneously and because the development of fruits occurs rapidly, the fruiting curve is similar to the flowering curve for herbaceous plants. It is because of the large number of herbaceous plants which have these nearly synchronous flowering and fruiting curves that the fruiting curve for all species so closely matches the flowering curve for all species.

Trees. The number of species of large and medium-sized trees in flower increases with the onset of the dry season, reaches a peak in February, but does not decrease until sometime in May (Fig. 3B). Species of larger trees in fruit do not reach their peak number until April, two months after the peak of flowering. The general level of fruiting remains rather high during June, July, and August at which time the number of species in flower is at its lowest.

These data contrast slightly with Allen's records of 280 species from Golfo Dulce, Costa Rica, presented by Janzen (1967: 625). A graph of the number of species in flower or fruit per month agrees with my data in showing a February peak for the number of species in flower, but Janzen shows a March peak for the number of species in fruit in contrast to an April peak for central Panama. One can not directly compare the data, since no attempt has been made to separate Allen's records into various habit components in the manner in which they are presented in this paper. However, the species recorded by Allen were principally arboreal.

Work by Fournier and Salas (1966) with 100 chiefly arboreal species from Villa Colón, San José Province, Costa Rica, indicates that in areas with a longer dry season (approximately one month longer than Panama) flowering periodicity is considerably different with two pronounced peaks, one during February and another during March and April.

The total number of tree species in flower on Barro Colorado Island may never be more than 78. Even in their peak month (February) they are surpassed in number by all other components of the vegetation. Nevertheless, because of their dominant habit and often conspicuous flowers, it is chiefly the larger trees which have formed the common impression among biologists working in Panama that February is the month of maximum flowering and that the peak of fruiting is delayed until the latter part of the dry season and early wet season.

Small Trees and Shrubs. For small trees and shrubs the small July burst of species in flower is followed by a maximum number of species in fruit in August (Fig. 3C). After these peaks both flowering and fruiting decline to their lowest point in November. Then a gradual increase occurs in the number of species flowering per month until a maximum is reached in March. The March peak of flowering is followed by an insignificant peak of fruiting in April after which fruiting tapers off sharply to a low point in May. The one-month lag in the peak of fruiting for shrubs and small trees, in comparison to a two-month lag for the larger trees, reflects the smaller size of fruits for most shrubs and small trees.

Woody Vines. Woody vines apparently react more quickly to the dry season than do the large trees. The increase in the number of species in flower is greater than that of the large trees for the months of December and January. While they reach their peak of flowering activity in February and thus coincide with the flowering peak of the large trees, their fruits as a rule develop more quickly than those of the trees. Consequently the peak of fruiting for vines is also in February. In this regard it is interesting to note that 66% of all vines fruiting in the dry season are wind dispersed, while the comparable figure for large and medium-sized trees is only 36%. This explains why the vines must flower earlier and produce their fruits earlier than most large trees. If the wind-dispersed plants are to take advantage of the high wind intensity of the dry season, they must flower early in the dry season and develop their fruits quickly. In the case of species with larger fruits, such as many bignoniaceous vines, they must flower in the wet season so that their fruits are mature during the dry, windy period. Since most wind-dispersed fruits are light in weight they are able to develop quickly. Vines, unlike herbs and the sub-canopy trees and shrubs, do not show an appreciable increase in flowering in July.

Despite the fact that the burst of flowering activity in the dry season figures prominently for all major components of the vegetation, it may be that neither the dry season nor the wet season is more important as an optimum period for reproduction. There is almost the same number of species which have at least some flowers in the dry season as for those which have at least some flowers in the wet season. The same is true for fruits. In all cases the figure is nearly 800 species.

Even if we include only those species whose flowers or fruits are restricted to a particular season and those flowering more than nine months which have peaks occurring in a particular season, we still have very similar figures. These are all in the neighborhood of 220 species in each case.

In a very restricted sense — excluding all species flowering more than nine months — there is still a nearly identical number of species flowering in the dry season and in the wet season. There are 143 species for the dry season and 144 species for the wet season. In the same sense there are 128 species with fruits in the dry season and 154 with fruits in the wet season.

While there is an insignificant difference in the total number of species fruiting in the dry season *versus* those fruiting in the wet season, the morphology of their fruit is important. It was found that the dry season contained 86 species (39% of the total) whose fruits were adapted for wind dispersal and 83 (37%) which were adapted for dispersal by animals. The wet season on the other hand, had 19 (8% of the total) species with fruits adapted for wind dispersal. There were 166 fruits (73%) which were adapted for dispersal by animals. These figures are based only upon those species whose fruiting was restricted to either the dry season or the wet season or which had their peak of fruiting restricted to either the dry or wet season.

Thus, although there is a definite peak of activity for flowering and fruiting in the dry season, the longer length of the wet season, coupled with a significant peak in July, apparently makes the difference between the two seasons insignificant

in terms of the total number of species which utilize each for reproduction. It may be seen however, that the dry season is more important from the standpoint of the reproduction of the total number of individuals.

An attempt to characterize the total seasonality picture of any family, *i.e.*, including the seasonality of both flowers and fruits for each species, is very difficult. However, it is possible to generalize in the case of a few families.

Included among families which I consider to be generally dry season families on Barro Colorado Island are: Anacardiaceae, Acanthaceae, Bombacaceae, Cochlospermaceae, Combretaceae, Lauraceae, Marcgraviaceae, Theaceae, Tiliaceae, Turneraceae, Violaceae and Vochysiaceae.

Families which flower predominantly in the wet season are: Amaryllidaceae, Burmanniaceae, Gesneriaceae, Haemodoraceae, Marantaceae, Musaceae and Zingiberaceae. With the exception of the Gesneriaceae, all of these wet season families are monocots.

Families tending to flower all year are the Caryophyllaceae, Commelinaceae, Curcurbitaceae, Passifloraceae, Scrophulariaceae, Solanaceae, Umbelliferae and Vitaceae.

It is important to point out that all of the data presented in this paper deals with the seasonality of the species not individual plants. Given enough collections of a particular species from any area, we can perhaps determine adequately the seasonality of that species. Yet we will know nothing of the flowering season of individual plants without field observation. While some species flower at about the same time each year, individual plants need not flower each year. Reports of plants which flower every two years are common, and other species are known to flower at much longer intervals (Corner, 1952; Richards, 1966). Though it can not be determined from the study of herbarium specimens, some species may flower at regular intervals of more than or less than one year but with no relation to a calendar year. While a bimodal species may flower twice a year, individuals of the species may flower only once each year. Long-term observations are sorely needed on many species to determine the seasonality of individuals of a species.

SUMMARY

While 13% of the angiosperms occurring on Barro Colorado Island in central Panama apparently flower continuously without pronounced peaks, most plant species have seasonal flowering behavior. The species have been classified into seasonality groups, the largest consisting of those species which have most or all of their flowers and fruits in the dry season; those which flower and fruit in the dry season but also in the early wet season; those which have most or all of their flowers and fruits in the wet season; and those which flower and fruit in the wet season but also in the early dry season. Over 40% of the species have flowering periods which are as much as nine months long, but the majority of these have a definite period of peak activity. This period was used to classify these species into seasonality groups.

More species were transitional, utilizing both the dry and the wet season to flower and fruit, than were restricted to either the dry or wet season exclusively.

The peak flowering period for all major components of the vegetation was found to be the dry season. The period following the resumption of the rains (particularly June) showed the least flowering activity. This was probably due to intense vegetative competition of most or all species.

The herbaceous plants flowered most quickly in response to the onset of the dry season with a peak of flowering in December. They were followed by the woody vines and trees with peak flowering in February, then by the small trees and shrubs with a peak in March.

Woody vines, though reaching their peak of flowering with the tall trees, respond more quickly to the dry season and produce their fruits more quickly than the tall trees. They were also found to contain a higher percentage of wind-dispersed fruits than did the tall trees.

The respective fruit size and development time of the various components of the vegetation is reflected by the lag in the peaks of fruiting in comparison to flowering. A one-month lag was seen in the fruiting peak of the small trees and shrubs and a two-month lag in the fruiting peak of the taller trees.

Despite the fact that all major components of the vegetation have their flowering peak in the dry season, this may prove to be no more important than the wet season from the standpoint of reproduction. Although no information is yet available on the number of individuals flowering in each season, it has been determined that as many species flowered and fruited during the wet season as did in the dry season. Those species flowering chiefly in the dry season did differ, however in having a much higher percentage of wind-dispersed fruits.

While the data presented here is general in nature and may have posed more questions than it has answered, it is hoped that it will provide an impetus to further research in tropical phenology. This subject is beginning to get some of the attention it deserves, but much work is needed before we will begin to understand the significance of seasonal fluctuations in the tropics.

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STUDIES IN NEOTROPICAL PALEOBOTANY. I. THE OLIGOCENE COMMUNITIES OF PUERTO RICO[1]

ALAN GRAHAM[2] AND DAVID M. JARZEN[2, 3]

ABSTRACT

Studies are being made of plant microfossils from seven Tertiary formations in Mexico, Panama, and Puerto Rico. The Puerto Rican samples from the Oligocene San Sebastian Formation have yielded 165 morphological forms; 44 have been identified, and 15 of these have no previously known fossil record. Community types include a coastal, brackish-water assemblage of *Rhizophora* and *Pelliciera*, an upland tropical to subtropical community, and an arboreal cool-temperate community of *Fagus*, *Liquidambar*, and *Nyssa*. Of the 44 genera identified, 31 presently grow in Puerto Rico, three grow on other islands of the Antilles, seven are found in ecologically comparable habitats elsewhere in Latin America, and only the three temperate trees require habitats not presently available on the island. The temperate element suggests altitudes greater than those of today, and recently available geological data reveal the presence of Oligocene highlands of 13,000 to 15,000 feet elevation. These would be sufficient to provide cool-temperate conditions in an insular environment at 18 degrees north. Ancestral Puerto Rico (Hispaniola, Puerto Rico, and the Virgin Islands) provided an effective landbridge between northern South America, the West Indies, and Mexico (Yucatan). However, the Oligocene seas extended across at least part of peninsula Florida and up to 120 miles inland along the Texas Gulf Coast; thus the barrier to migration from the Antilles into southeastern North America was probably greater than at present. Of the 44 genera identified all have affinities with northern South America, eastern Mexico, and the Antilles; and none have exclusive affinities with the vegetation of southeastern North America. Studies from Panama and Veracruz, Mexico, suggest tropical elements in the modern and fossil floras of southeastern North America were introduced along an Isthmian-coastal Mexico route during the early Tertiary or subsequently through long-distant dispersal into tropical outliers (southern peninsula Florida).

The tropics are generally recognized as an important center for biological diversity, and a number of studies are underway dealing with the systematics, ecology, and evolutionary aspects of tropical plant communities. The more recent

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These studies began while one of the authors (AG) was a postdoctoral fellow in the Evolutionary Biology Program, Harvard University. Sincere gratitude is expressed to Reed C. Rollins, Director of the Program, and especially to Professor Elso Barghoorn in whose laboratory the work was initiated. R. A. Howard was frequently consulted about the modern vegetation of Puerto Rico. Rolla and Alice Tryon provided helpful suggestions on the ferns, and G. J. Gastony supplied ecological and floristic data for Pico Duarte, Dominican Republic. Other individuals providing information on special plant groups are Donald E. Stone (*Engelhardia*), Peter H. Raven (*Hauya*), and Grady L. Webster (*Alchornia, Tetrorchidium*). The authors also acknowledge courtesies extended by the staff of the herbaria and libraries of Harvard University, the University of Michigan, and the Smithsonian Institution. On matters of geology, W. H. Monroe, Othmar Tobisch, and especially R. P. Briggs, U.S. Geological Survey, San Juan provided much helpful information.

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paleobotanical record also constitutes an important source of data relating to the environment and environmental change under which the biota has diversified, pathways of migration, interchange between the North and South American communities, and former occurrences of species now disjunct or allopatric in distribution. Unfortunately even less is known about the geologic history of tropical American biotas than the modern associations. Although several recent studies on Cenozoic deposits have been made (Bartlett, 1967; Cogwill *et al.*, 1966; Gonzalez-Guzman, 1967; Heusser, 1961, 1964, 1966; Germeraad, Hopping & Muller, 1968; Langenheim, Hackner & Bartlett, 1967; Tsukada & Deevey, 1967; Hammen, 1963, 1964; Hammen & Gonzalez, 1960; Hammen & Wijmstra, 1964; reviews by Archangelsky, 1968; Menendez, 1969) and others are underway, there still have been more Tertiary palebotanical studies made in the western United States than in the rest of the Western Hemisphere south of the United States. Indeed there have been more revisions of fossil floras of the Columbia Plateau than combined Tertiary paleobotanical studies in the countries of Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, the Guianas, Ecuador, Paraguay, Uruguay, and Peru.

Among deterrents to traditional (*viz.*, megafossils) paleobotanical research in tropical regions have been the difficulty and uncertainty of obtaining researchable materials. Geologic maps may reveal the location of fine-grain, black shales associated with coal seams or continental shales of volcanic origin, but there is no certainty these beds will yield plant megafossils. However, rock types such as peat, lignite, and coal commonly contain pollen and spores. A total of 281 samples have been collected from Tertiary formations in Mexico, Panama, and Puerto Rico (Fig. 1), and about 75% yielded well-preserved plant microfossils. In many Latin American countries these rock types are important as a low-cost source of fuel, and consequently their age and distribution is frequently better known than for economically less important deposits. Thus the initial phases of these investigations concentrate on the palynology of lignites, while reconnaissance continues for supplementary megafossil sites.

The practical necessity of beginning with palynology and lignites presents difficulties that affect interpretation of the data. Fossil pollen and spores most commonly can be identifed only to genus—in a few cases to species, but in others only to family. Further, study of either the micro- or megafossil community provides only a part of the potential species composition. In a Miocene flora from southeastern Oregon (Graham, 1963, 1965*a*), 16 genera (27% of the flora) were represented as microfossils but were absent from the megafossil assemblage, and 10 genera (17%) were found only as megafossils. Since the species list is the basis for interpretation of fossil floras, the necessity of considering only the palynology of these Latin American deposits is a limiting factor of some consequence. Another problem is facies control of the microfossil composition. Lignites in warm-temperate regions are formed under brackish-water, coastal environments and commonly contain 75–95% *Rhizophora* pollen. Thus the samples are biased toward strand vegetation and may provide little data on communities removed from the basin of deposition. This difficulty recently has been overcome to some

extent in the Panamanian and Puerto Rican deposits by obtaining pollen-bearing samples of different lithologies associated with the lignites. Other problems include the inadequacy of existing reference collections for identification purposes and the lack of pertinent literature on the distribution and ecology of tropical plants once the microfossils have been identified. Although these difficulties presently require conservative interpretation of data and tentative conclusions, even preliminary investigations can yield data significant in comparison to our present state of knowledge.

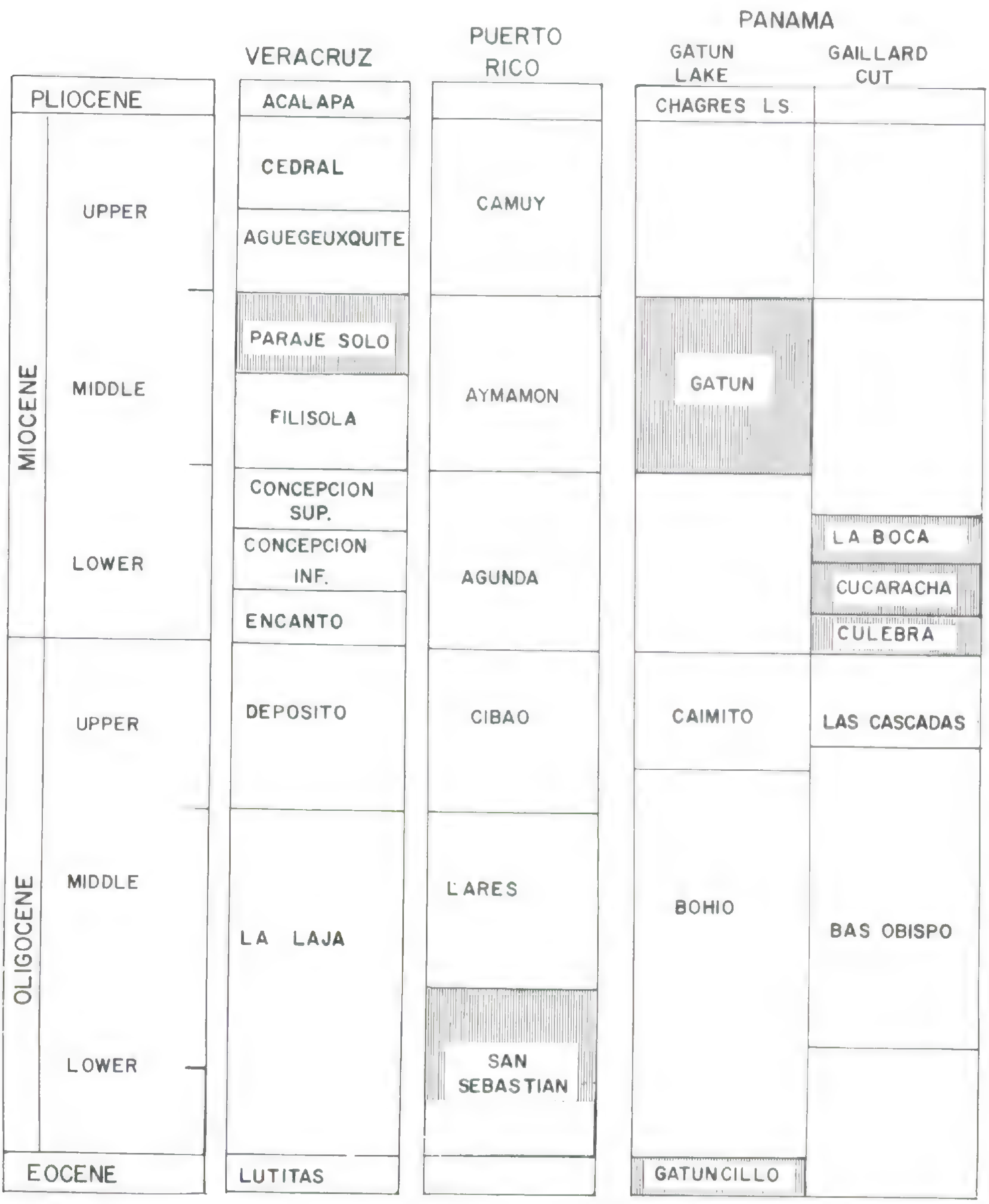

FIGURE 1.—General stratigraphic position of Tertiary formations in northern Latin America included as a part of "Studies in Neotropical Palcobotany."

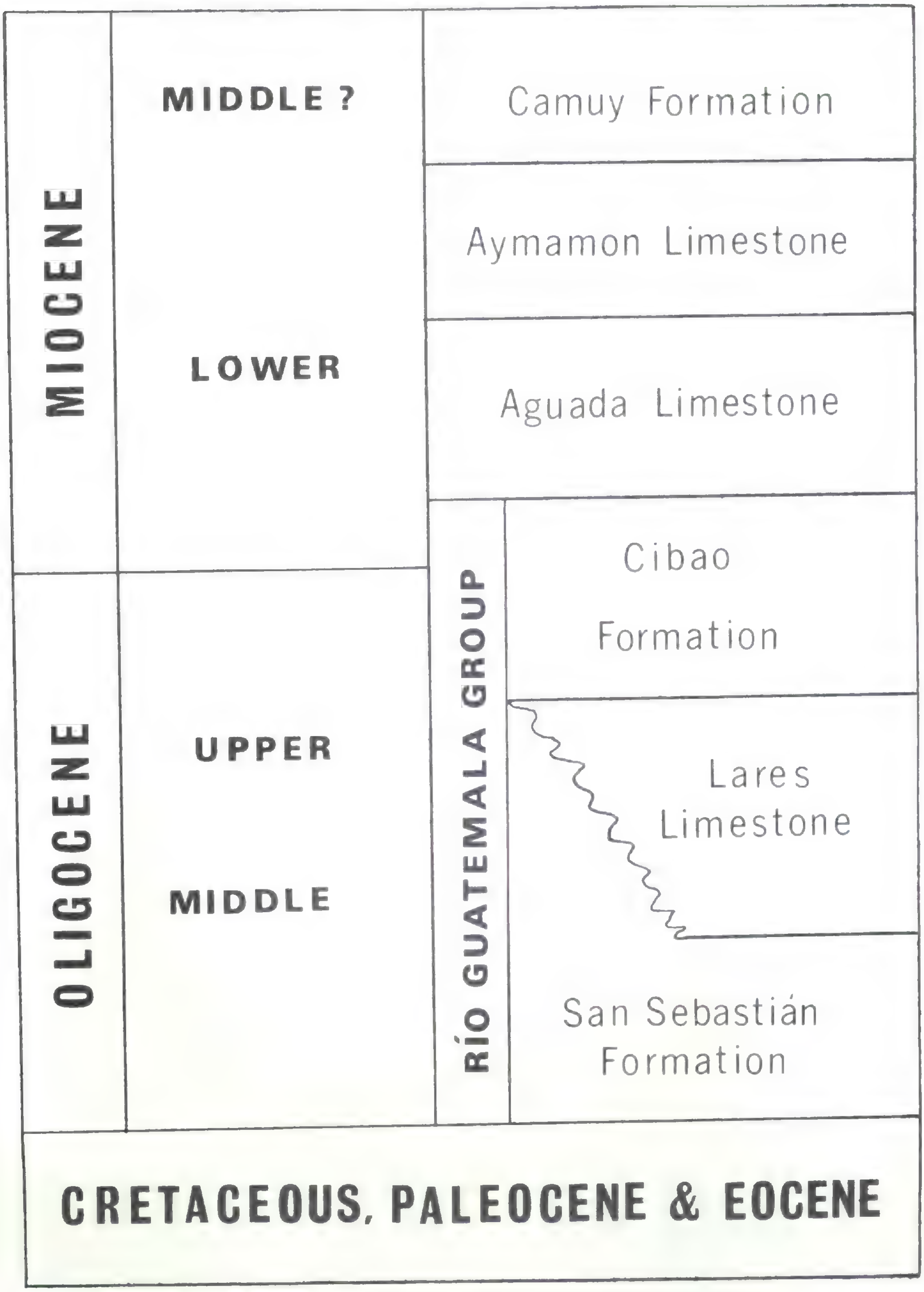

FIGURE 2.—Stratigraphic relationships of the San Sebastian Formation to other Oligocene and Miocene strata of Puerto Rico.

There is no published palynological information dealing with the Tertiary vegetation of the Antilles, and only a single paper (Hollick, 1928) treats plant megafossils. The usefulness of such data to an understanding of vegetational history in northern Latin America, and the origin of certain floristic affinities between North and South America is evident from the position of the islands. Forming an arc extending nearly from the Yucatan Peninsula eastward toward the Florida Keys and Bahama Islands, then curving south to the island of Trinidad, the islands are geographically suited to act as a land bridge between North and South American biotas.

Puerto Rico is the smallest and most easterly island of the Greater Antilles, located between 18° and 18° 30′ north and 65° 30′ and 67° 30′ west, with an area of 3,435 square miles. Average rainfall for the island ranges from over 180 inches in the eastern Cordillera to about 10 inches along the southwestern coast. Mean annual temperatures range from 78° F along the south coast to 70° F in the mountains. Recent accounts of the climatology and physiography of Puerto Rico are given by Banyon (1968, 1969), Pagney (1966), and Pico (1950, 1963). There are numerous accounts of the geology of Puerto Rico including those of Berkey (1915, 1919), Butterlin (1956), Hubbard (1920, 1923), Maury (1929), Meyerhoff (1933), Mitchell (1954), Zapp, *et al.* (1948), Kaye (1956), and Mattson (1967).

The study sites are located in the northwestern portion of Puerto Rico and have a base of tuffaceous sandstone and siltstone of Cretaceous, Paleocene, and Eocene age (Monroe, 1968). The San Sebastian Formation lies unconformably on this basement of Eocene strata and outcrops at several locations. The formation ranges in thickness from less than 1 m to 155 m and consists of sand and gravel, lignites and lignitic clays, and thin lenses of clay and very sandy clayey limestones. Above lies the Lares Limestone, and in places it becomes a facies equivalent of the San Sebastian Formation. The relationship between the Lower and Middle Tertiary formations of Puerto Rico in the vicinity of the collecting sites is shown in Fig. 2 (Briggs; Monroe, personal communication, 1969). The San Sebastian and Lares Limestones are considered Middle Oligocene, and thus the microfossils represent vegetation existing within the Greater Antillean Arc approximately 45 million years ago.

Materials and Methods

Lignitic clays and coal deposits containing well-preserved plant microfossils were obtained from outcrops of the Oligocene San Sebastian Formation, recently mapped by Briggs and Akers (1965). A collection of 50 samples was made from three localities designated PRL (Puerto Rican Lignites) A, B, and C (Fig. 3).

Locality PRL-A is on a small east-facing slope at the junction of Puerto Rican Highways 111 and 124, just west of Lares at the 35.3 km marker. The slope pinches out from north to south from a width of 20 22 feet to less than one foot. Two thin beds, 10 in. thick, of dark organic sediment are exposed. The upper bed is lignitic clay, with occasional lignite or brown coal interbedded in small quantities. The lower bed is a coarse steel grey lignitic sandstone with abundant invertebrate remains (calcareous shells). Samples 1–10 were collected from the upper lignitic clay, and samples 11–13 were made from the lower lignitic sandstone. All samples contained plant microfossils.

Locality PRL-B is on a new east-facing slope resulting from construction of a by-pass around the town of Lares. This by-pass to Highway 111 runs approximately NNE and is

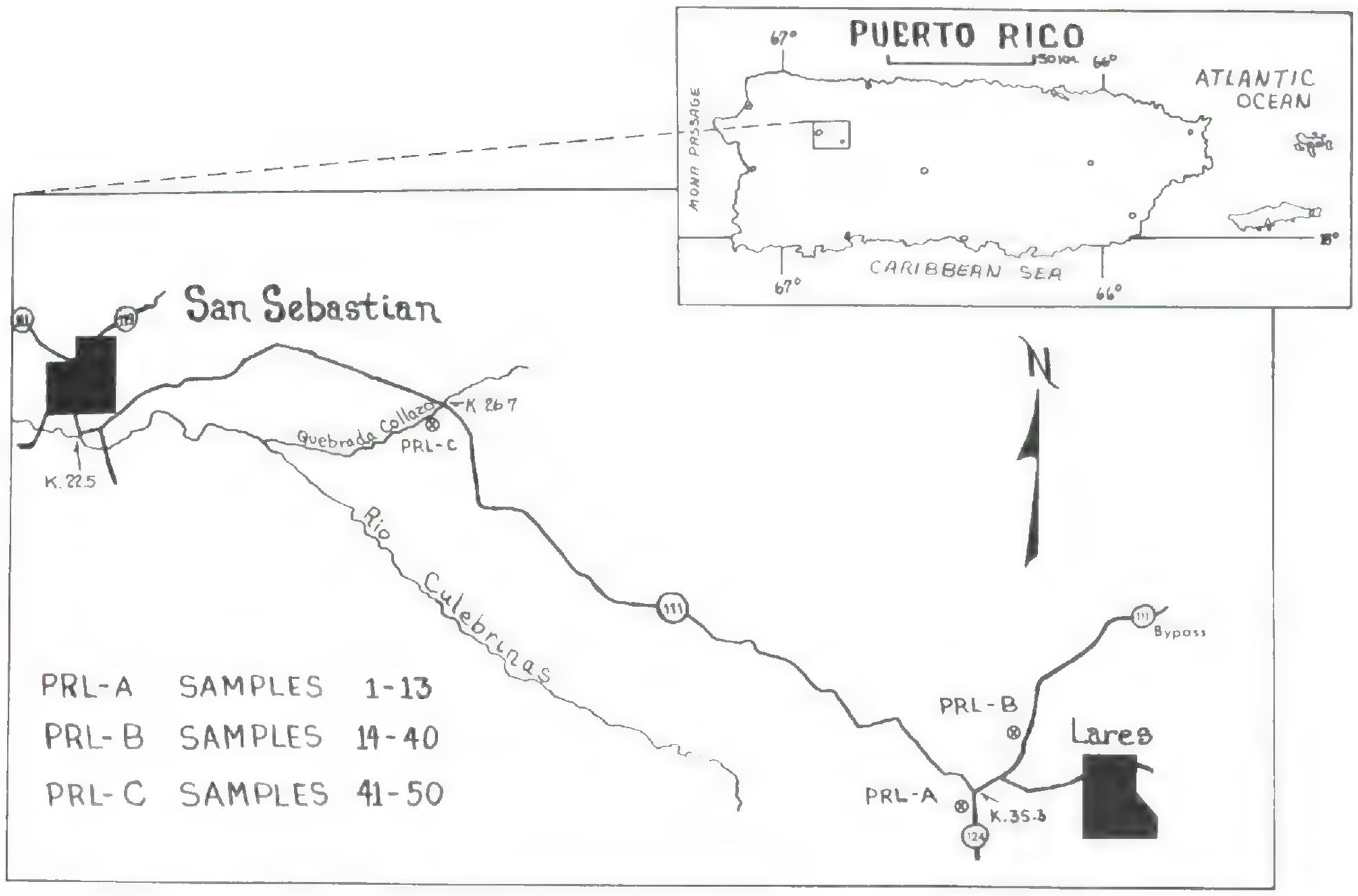

FIGURE 3.—Index map of Puerto Rican lignite localities.

adjacent to the east-facing slope. Samples 14–40 were collected from this locality (Fig. 4). The bluff is 40–45 feet high from the road base and is interbedded with alternating coal, coaly lignite, and lignitic clay.

Locality PRL-C is on the Collazo Quebrada at the base of the second falls below the San Sebastian-Lares bridge, at the 26.7 km marker. The bridge is approximately 4.2 km from the town of San Sebastian on Highway 111. This is the same site mentioned by Hollick (1928) as "Collazo River, near (or 'at') base of second falls below Carretara bridge." Samples 41–50 were collected from a lignitic clay about one foot thick containing abundant cuticles which curl from the surface of the rock upon drying; the matrix readily crumbles. Lenses of lignitic clay were also described from the base of the first falls (Hubbard, 1923) and at several other sites, but slumping and accumulation of debris have obscured these localities.

Samples were cleaned to expose unoxidized surfaces, macerated and covered with 48% HF for 24 hours to remove silicates. This was followed by 10% HCl to remove carbonates. Schultze Solution was used for 15–20 minutes to oxidize organic constituents. Separation of organic and residual inorganic fractions was by heavy-liquid flotation using $ZnBr_2$ adjusted to a specific gravity of 1.8 and centrifuged at 2000 rpm for one-half hour. The float fraction was acetolized and mounted unstained in glycerine jelly. Fifteen slides from each sample were prepared and sealed with diaphane. Photographs were made with a Wild microscope equipped with a Nikon 35 mm camera and were mounted on Burroughs Y-9 Unisort Analysis Cards for reference.

Comparison of fossil types with modern material was made from the reference collection of about 12,000 species at Kent State University. Additional collections of modern material were made as necessary from specimens in US. All slides from Locality C and three to five slides from Localities A and B were scanned for morphological types. Estimates of relative abundance were made by tabulating the first 200 recognizable types, and these are listed as rare (0.5% or less), common (0.5–15%), or abundant (greater than 15%).

Once the fossils were identified, distribution maps were prepared showing the range of the modern counterparts. Distribution and ecological data were obtained from the literature (*e.g.*, Standley, 1920–1926, 1928; Little & Wadsworth, 1964; Alain, 1963, 1968; Gleason

& Cook, 1926; Howard, 1962, 1966; Allen, 1956) and from herbarium sheets at US and GH.

All slides, photomicrographs, and other data relevant to the study are on deposit at the Palynology Laboratory, Kent State University.

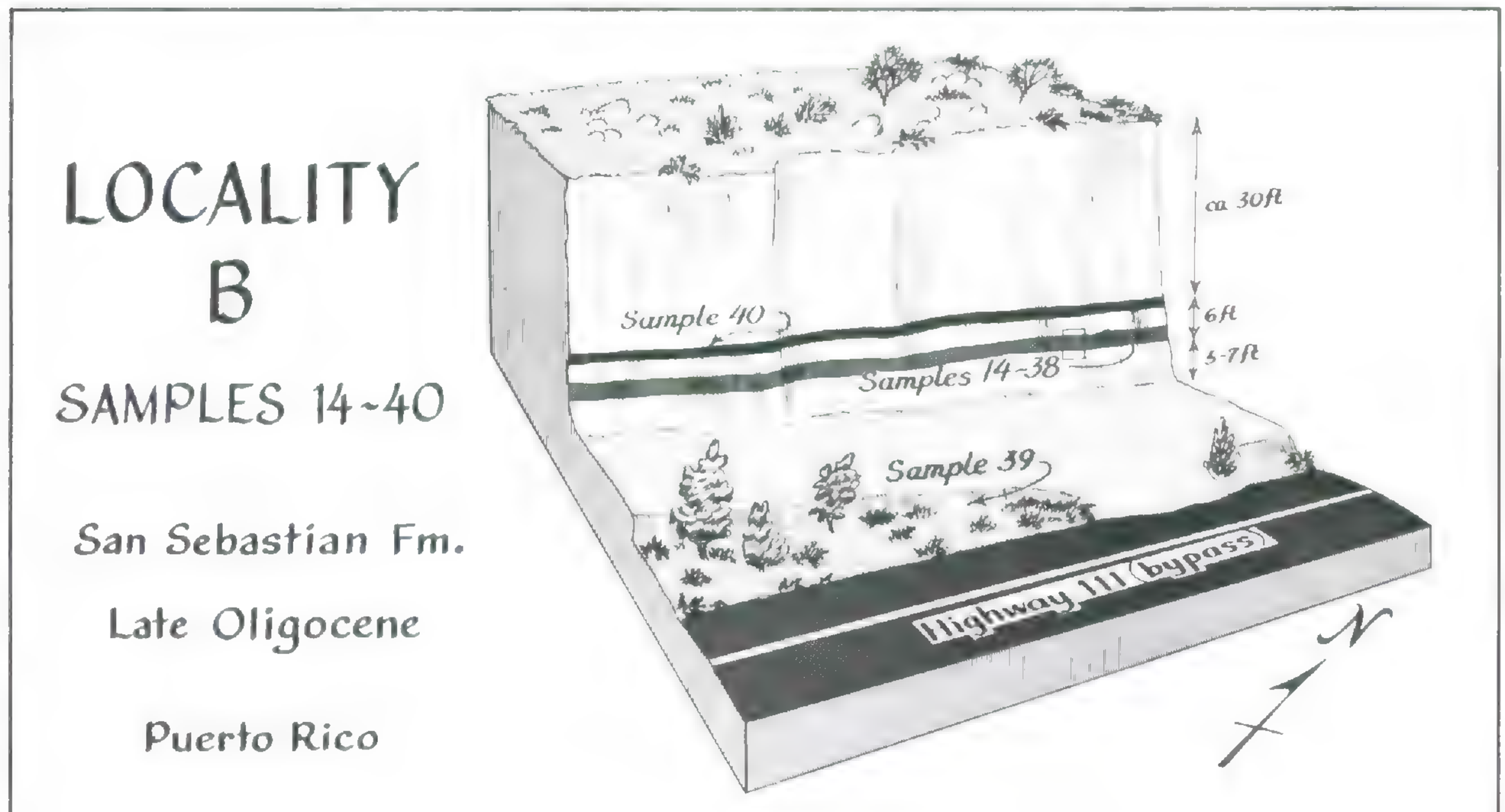

FIGURE 4.—Stratigraphy, sequence of lithologies, and position of samples from Locality B, San Sebastian Formation, Puerto Rico.

Systematics

A total of 165 morphological types of pollen and spores were recovered from the San Sebastian Formation. From this assemblage 44 (ca. 25%) have been identified to genus. In the following discussion the palynomorphs are cited according to locality (A, B, or C) and sample number (1–50). The photomicrographs are cited according to locality, sample number, and slide number (1–15), and coordinates of the England Slide Finder are also given. A summary of relative abundance is given in Table 1 and the species composition of the San Sebastian microflora in Table 2. Detailed descriptions are deferred to a later publication where the microfossils will be given formal taxonomic status.

Lycopodium (Fig. 5–6)

The genus *Lycopodium* consists of approximately 100 species widely distributed throughout tropical and temperate regions of the world. The spores of many temperate forms and those most frequently reported from Cenozoic deposits in the Northern Hemisphere are characterized by a distinct reticulum on the distal surface. Certain tropical species differ, however, in having slightly protruding, broadly blunt apices and/or a rugulate to less distinct reticulate sculpture pattern. The spores of *Lycopodium* Type A are similar to those of *L. carolinianum*. They were recovered from samples C-43 and C-50, with an abundance of 0.5%.

The spores of *Lycopodium* Type B are most similar to the modern *L. serratum*. Although we did not see collections of the plant from Puerto Rico, it does occur on Cuba and Haiti. Single specimens were recovered from samples C-48 and C-50.

Selaginella (Fig. 7)

Members of the genus *Selaginella* number about 700 species and are chiefly tropical in distribution, with a few ranging into temperate regions. At least three species are recorded from Puerto Rico, *S. laxifolia, S. krugii,* and *S. substipitata.* The spores are rare in the San Sebastian microflora and occur at Localities B and C.

Cyathea (Fig. 8)

The genus *Cyathea* is a tropical to subtropical assemblage of approximately 800 species. It is an arborescent fern of the wet tropics especially in the mountainous regions from Mexico to Chile. In the Antilles it occurs on all the islands and is represented by about 35 species including *C. arborea, C. borinquena,* and *C. pubescens. Cyathea arborea* is the most widespread and is abundant on Puerto Rico. The plants are common secondary invaders of impoverished soils in damp climates, especially at lower altitudes (Richards, 1966: 398).

The fossil spores range in size from 35 to 55μ, suggesting more than one species may be represented. They are present in Locality B, samples 15, 19, 25, and 33 with an abundance of 0.5–1.5%, and in Locality C, samples 41, 43, and 50 with an abundance of 0.5–1.0%.

TABLE 1. Per cent composition of identified taxa from San Sebastian Formation (Oligocene), Puerto Rico (based on 200 grains counted). P = present.

Taxon	Locality A						Locality B					Locality C				
	3	4	8	10	12	13	15	19	25	33	40	41	43	45	48	50
Lycopodium A													.5			.5
Lycopodium B															P	P
Selaginella												P			P	P
Cyathea							1		.5	1.5	.5		.5	1		.5
Hemitelia (*Cnemidaria*)															P	
Jamesonia (*Eriosorus*)																
Pteris (A,B,C)							5		.5		.5			P		
Podocarpus												P		P		
Abutilon																
Acacia				.5									.5	P		
Aetanthus																
Alchornea	.5			1		1	1		.5	1		1	.5	.5	.5	.5
Bernoullia												.5	.5	5	2.5	1
Bombax																
Brunellia											P		1		1.5	
Bursera																
Casearia																
Catostemma				.5								P	2.5	1	P	1
Chrysophyllum									.5			P				
Corynostylis								.5					.5			.5
Dendropanax															P	
Engelhardia	1.5		1		2	2.5	15	3	2.5	.5	.5	44.5	31	54	41.5	37
Eugenia												.5		P	.5	
Fagus	1															
Faramea									1.5			P				
Guarea												.5	P	P	.5	
Hauya													.5		P	
Ilex																
Jacaranda																
Liquidambar													1.5	.5	2	.5
Marcgravia																
Merremia													.5			
Myrica																
Norantea																P
Nyssa	.5											.5	1.5		4.5	.5
Oxalis																
Pelliciera		2	1	1	1	P					P				P	
Pleodendron												.5	.5			.5
Rauwolfia																
Rhizophora	89	95	96	95.5	47.5	36	1	77	61.5		71	.5	.5			1.5
Salix													1		.5	
Tecoma																
Tetrorchidium					.5		1.5	2		.5		P	3	1	1	.5
Tournefortia					P											
Zanthoxylum							.5					1.5				P
Monolete Fern Spores (Polypodiaceae)					2	6.5	9	5	5	30	5	12	18	10	8	5
Trilete Fern Spores	2				9	16	10	5	4	10	10	8	12	13	5	7
Palmae	1	2			3.5	3.5	8	5	7	50	2	5	15	9	12	12
Unidentified	4.5	1	2	3.5	32.5	34.5	48	1	15.5	8.5	11	24.5	8	6	19.5	31.5

TABLE 2. Systematic listing of identified genera occurring in the San Sebastian Formation, Puerto Rico.

Family: Lycopodiaceae	Genus: *Liquidambar*	Family: Violaceae
Genus: *Lycopodium*	Family: Oxalidaceae	Genus: *Corynostylis*
Family: Selaginellaceae	Genus: *Oxalis*	Family: Flacourtiaceae
Genus: *Selaginella*	Family: Rutaceae	Genus: *Casearia*
Family: Cyatheaceae	Genus: *Zanthoxylum*	Family: Rhizophoraceae
Genus: *Cyathea*	Family: Burseraceae	Genus: *Rhizophora*
Genus: *Hemitelia (Cnemidaria)*	Genus: *Bursera*	Family: Myrtaceae
Family: Gymnogrammaceae	Family: Meliaceae	Genus: *Eugenia*
Genus: *Jamesonia (Eriosorus)*	Genus: *Guarea*	Family: Onagraceae
Family: Polypodiaceae	Family: Euphorbiaceae	Genus: *Hauya*
Genus: *Pteris*	Genus: *Alchornea*	Family: Araliaceae
Family: Podocarpaceae	Genus: *Tetrorchidium*	Genus: *Dendropanax*
Genus: *Podocarpus*	Family: Aquifoliaceae	Family: Nyssaceae
Family: Salicaceae	Genus: *Ilex*	Genus: *Nyssa*
Genus: *Salix*	Family: Malvaceae	Family: Sapotaceae
Family: Myricaceae	Genus: *Abutilon*	Genus: *Chrysophyllum*
Genus: *Myrica*	Family: Bombacaceae	Family: Apocynaceae
Family: Juglandaceae	Genus: *Bombax*	Genus: *Rauwolfia*
Genus: *Engelhardia*	Genus: *Catostemma*	Family: Convolvulaceae
Family: Fagaceae	Genus: *Bernoullia*	Genus: *Merremia*
Genus: *Fagus*	Family: *Marcgraviaceae*	Family: Boraginaceae
Family: Loranthaceae	Genus: *Marcgravia*	Genus: *Tournefortia*
Genus: *Aetanthus*	Genus: *Norantea*	Family: Bignoniaceae
Family: Brunelliaceae	Family: Theaceae	Genus: *Jacaranda*
Genus: *Brunellia*	Genus: *Pelliciera*	Genus: *Tecoma*
Family: Hamamelidaceae	Family: Canellaceae	Family: Rubiaceae
	Genus: *Pleodendron*	Genus: *Faramea*

Previous reports of fossil spores of *Cyathea* include Hammen and Gonzalez (1960) from the Pleistocene of Colombia and Hammen (1963) from the Quaternary of Guyana. Megafossils have been reported by Berry (1922: 119) from the Miocene of Chile, Hollick and Berry (1924) from the Pliocene of Bahía, Brazil, and Pabst (1968) from the Chuckanut Formation (Paleocene?) of northwestern Washington.

Hemitelia (*Cnemidaria;* Fig. 9)

The taxonomy of the tree ferns is currently being revised, and there are nomenclatural differences between the older and newer systems. According to some treatments the arborescent ferns belong to the genus *Cyathea,* while others recognize a number of genera. In a forthcoming revision ferns previously recognized as *Hemitelia* will be called *Cnemidaria* (R. Tryon, personal communication, 1969). The plants are common to moist tropical mountains, and three species, including *H. horrida,* are native to Puerto Rico. They are occasional to rare, however, and usually do not reach tree size as do species of *Cyathea* (Little & Wadsworth, 1964). The genus is pantropical in distribution, and about 40 species are recognized (Fig. 69).

A single specimen of *Hemitelia* was found in sample C-48. Other reports are those of Hammen and Gonzalez (1960) from the Pleistocene and Holocene of Colombia, and the spores are common in our samples from the Miocene Paraje

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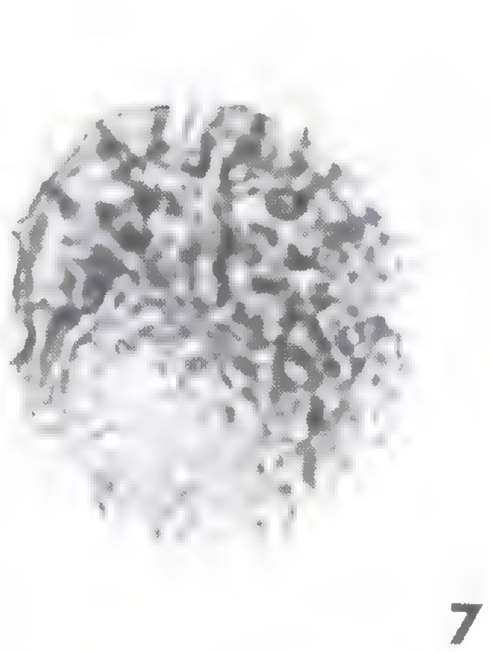

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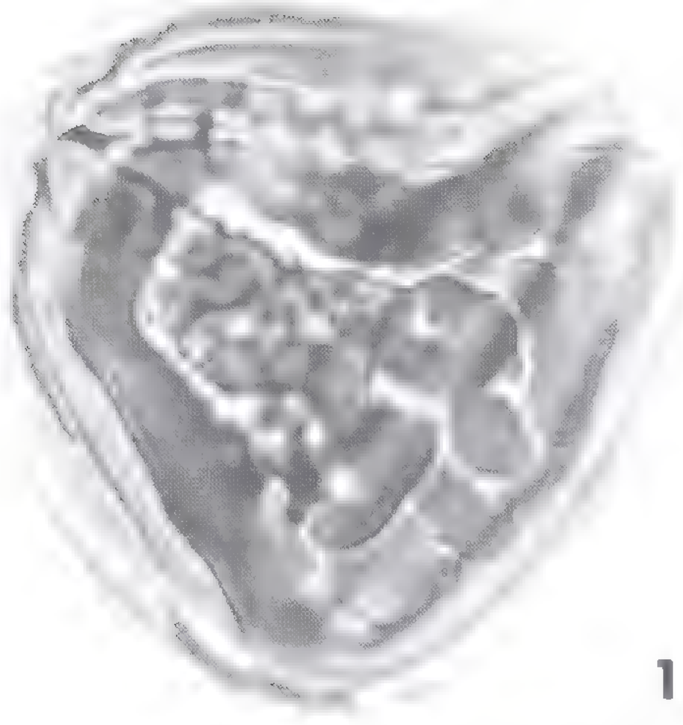

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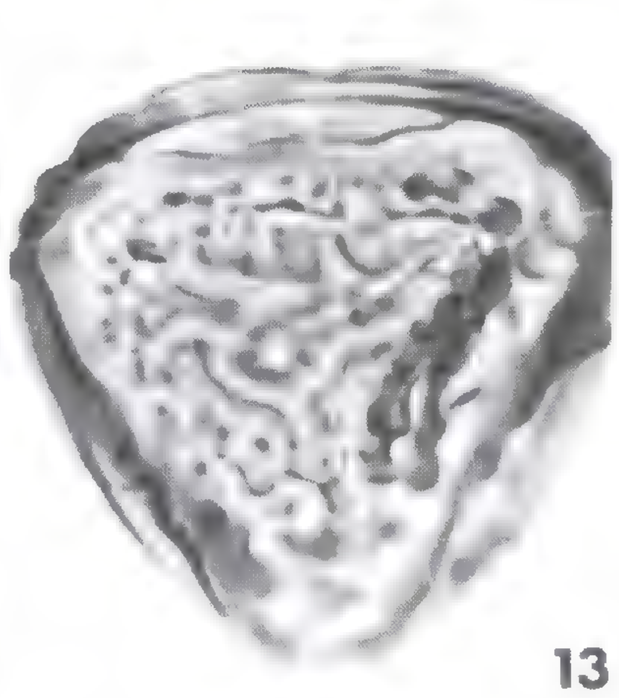

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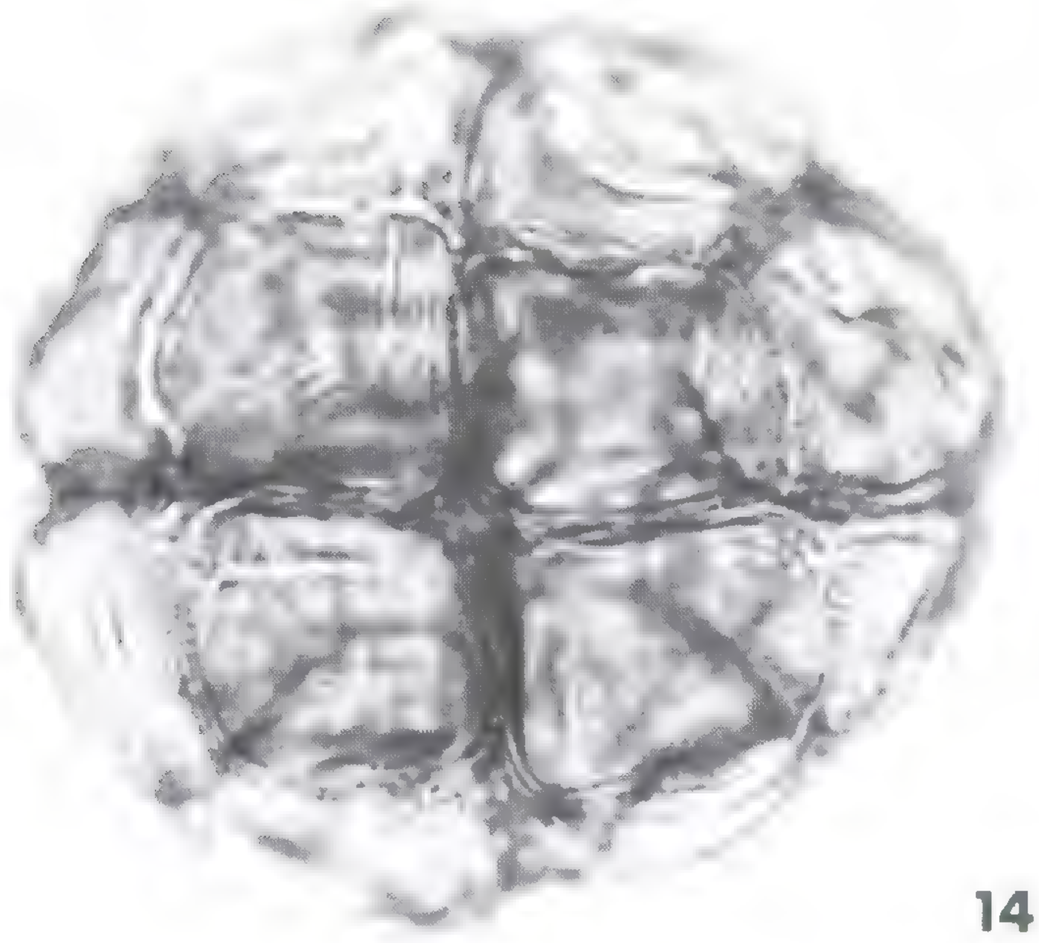

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Solo Formation of Veracruz, Mexico. Wolfe (personal communication, 1969) has megafossils, probably related to Asiatic forms, from Tertiary material in Alaska. Hollick and Berry (1924) described fossil fronds from the late Tertiary of Bahía, Brazil, as *H. branneri.* It was compared to *H. grandifolia* which is present today in the Antilles and tropical South America. Hollick (1928) also reported fronds of *H. branneri* from the Collazo Shales of Puerto Rico.

Jamesonia (Fig. 10)

The spores of *Jamesonia* are similar to *Eriosorus,* and the two genera are closely related (A. Tryon, personal communication, 1969). With limited fossil material generic identification is tentative, although the spore is most similar to *Jamesonia* among the genera represented in our reference collection. *Jamesonia* consists of about 19 species distributed from southern Mexico to central Bolivia and Brazil. It is a high altitude plant (1,500–5,000 m) of the paramos or other cool, wet highlands (Tryon, 1962); it characteristically grows at elevations higher than *Eriosorus.*

The genus *Eriosorus* consists of about 30 species occurring from Andean South America, Brazil, Bolivia, and on the sandstone massifs of Venezuela north to Guerrero, Mexico. *Eriosorus hispidulus* grows on the isolated Atlantic island of Tristan da Cunha (Tryon, 1966) and on El Yunque, Puerto Rico. It is a member of the wet cloud forest vegetation growing most commonly at elevations above 2,000 m.

A single spore of *Jamesonia* (or *Eriosorus)* was recovered from sample C-49. Spores of *Jamesonia* are reported from the Pleistocene and Holocene of Columbia (Hammen & Gonzalez, 1960), and *Eriosorus* is known from the Pleistocene of Tristan da Cunha (Hafsten, 1960).

Pteris (Fig. 11–13)

The spores of *Pteris* are common in the San Sebastian Formation. Several species are probably represented. Three relatively distinct types can be recognized, based on differences in sculptural elements on the distal surface. In Type A the sculpturing elements are a series of irregularly distributed sharp ridges; in Type B, low rounded ridges; and in Type C, verrucae.

The genus consists of about 250 species. At least some grow under relatively xerophytic conditions and may be primary invaders in dry barren regions (Richards, 1966: 271). Spores of *Pteris* are common at Localities B and C, being most abundant in samples C-43, 45, and 50, where they represent as much as 5%

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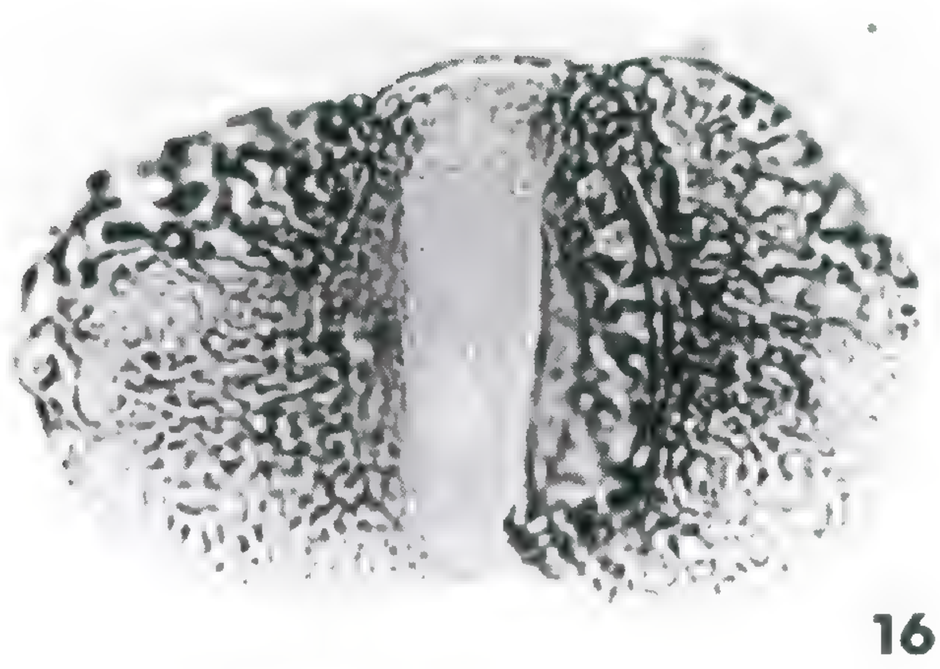
FIGURES 5–15.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 5. *Lycopodium* Type A, 40μ (C-50, 1; ESF Y-35). — 6. *Lycopodium* Type B, 40μ (C-50, 15; ESF O-21,3). — 7. *Selaginella,* 28μ (C-48,1; ESF N-28). — 8. *Cyathea,* 33μ (C-43,15; ESF B-45). — 9. *Hemitelia,* 42μ (C-48,1; ESF O-31,1. — 10. *Jamesonia (Eriosorus),* 44μ (C-49,1; ESF K-25,2). — 11. *Pteris* Type A, 54μ (C-42,1; ESF S-38,4). — 12. *Pteris* Type B, 43μ (C-44,5; ESF L-26). — 13. *Pteris* Type C, 45μ (C-46,2; ESF K-28,4). — 14. *Acacia,* 72μ (C-45,10; ESF J-38,3). — 15. *Bernoullia,* 59μ (C-48,10; ESF G-30).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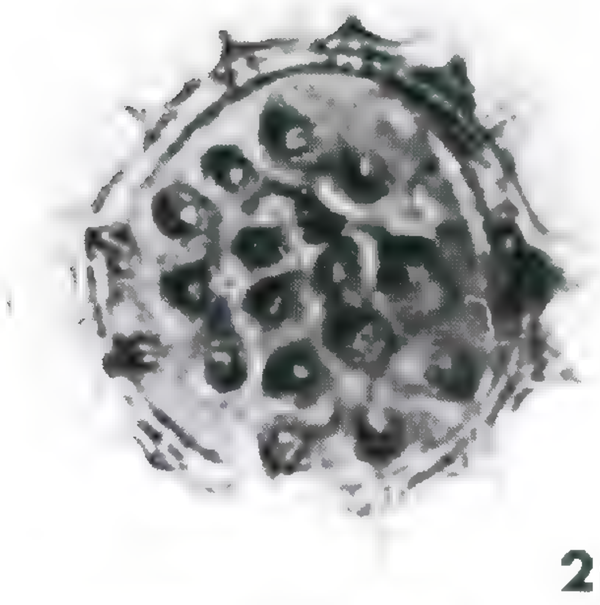
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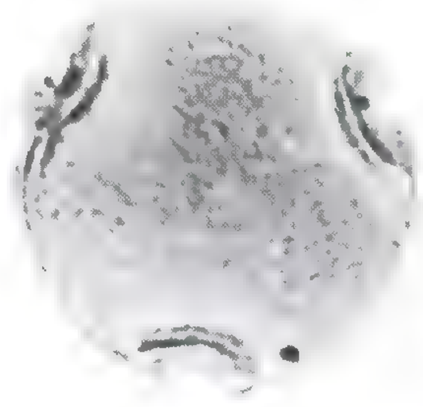
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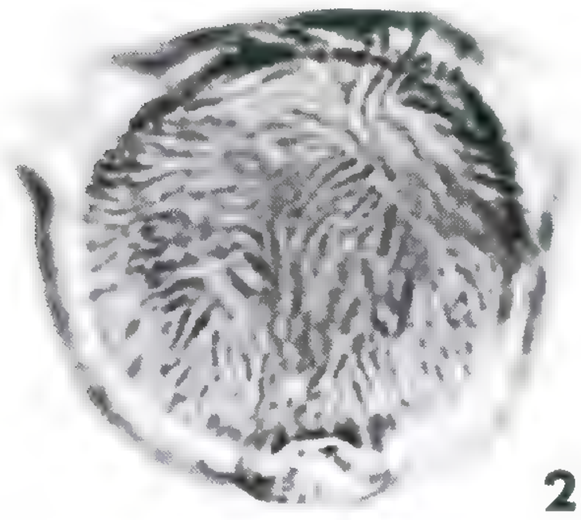
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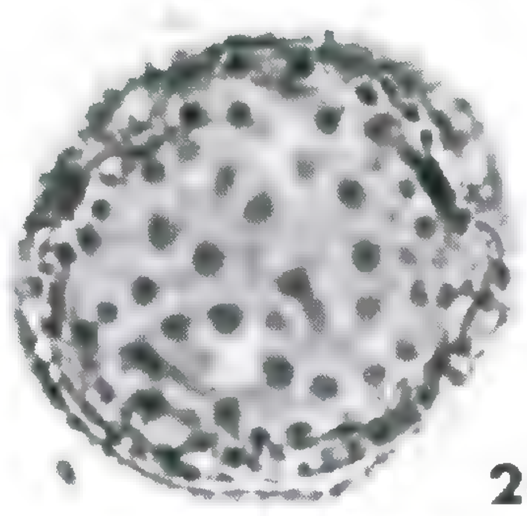
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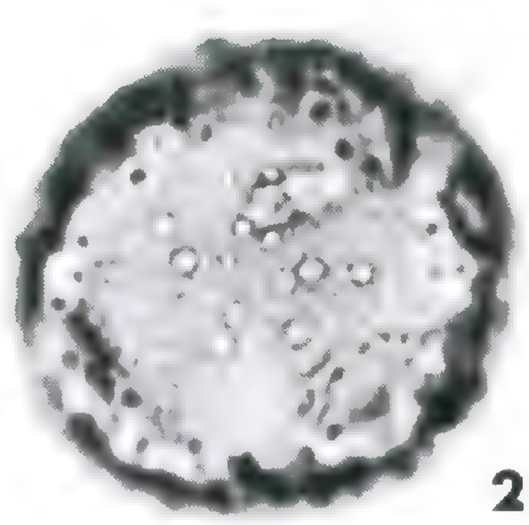
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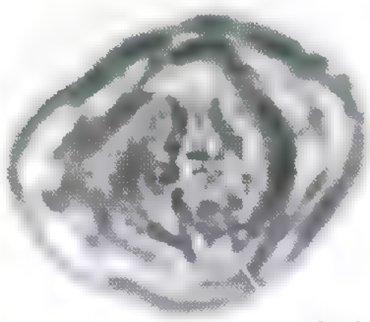
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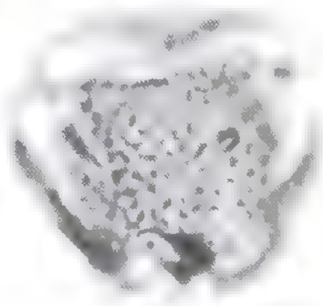
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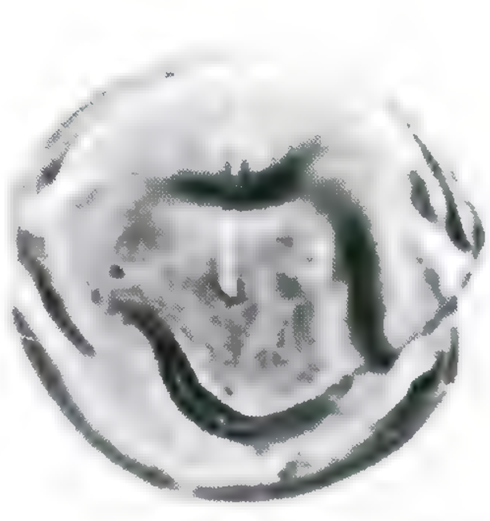
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of the total assemblage. Spores similar to *Pteris* have been reported by Hammen and Gonzalez (1960) from the Pleistocene of Colombia as *Triletes* "tipo J."

Podocarpus (Fig. 16)

The genus *Podocarpus* consists of about 100 species distributed primarily in the Southern Hemisphere. Sixteen species are known from Mexico, Central America, and the Antilles (Fig. 70). Among these, *P. coriaceus* occurs on Puerto Rico and is the only native conifer. The plants grow in high-mountain, tropical forests, although they are more abundant near the bottom of slopes in moister soil (Gleason & Cook, 1926: 115). It is a medium-size tree (ca. 10 m tall) and produces pollen nearly throughout the year (Little & Wadsworth, 1964).

Podocarpus pollen is rare, in the San Sebastian Formation, with only 3 or 4 grains recovered (samples C-41, 42, 45). Previous reports are those of Hammen and Gonzalez (1960) from the Pleistocene-Holocene of Colombia; Tsukada (1966) from core samples of Lake Petenxil, Guatemala, absolute date (C^{14}) 4,000 years before present; and Heusser (1966) from Late Pleistocene deposits in the Province of Llanquihue, southern Chile. The genus is also present in our samples from the Miocene Paraje Solo Formation of Veracruz, Mexico. Specimens of fossil wood and leaves of *Podocarpus* have been reported from the lowermost Miocene of Argentina (Berry, 1938), the Late Tertiary of Bolivia (Berry, 1939: 33), and the Eocene of western Tennessee (Dilcher, 1969). An account of the distribution of Podocarpaceae in Southern Hemisphere Cretaceous and Tertiary beds is given by Couper (1953).

Abutilon (Fig. 20)

The tropical to warm-temperate genus *Abutilon* (Malvaceae) consists of about 100 species of herbs and shrubs, widely distributed around the world. About 20 species occur in the Antilles with 4–5 in Puerto Rico. Species of *Abutilon* are adapted to a wide range of ecological conditions, including dry rocky slopes, streamsides, open plains, and more tropical shaded forest conditions. A single grain of *Abutilon* was recovered from sample A-1.

The fossil pollen is very similar to that of the modern *A. incanum*. This species is not found in Puerto Rico today, but grows in western Arizona, Texas, and southward into Baja California, Nuevo León, San Luis Potosí, and Sinaloa, Mexico, on dry rocky slopes (Shreve & Wiggins, 1964: 880). This distribution

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FIGURES 16–36.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 16. *Podocarpus*, 40 × 68μ (C-41,7; ESF U-37, 1–2). — 17. *Aetanthus* 32μ (C-46,1; ESF H-41,3). — 18, 35–36. *Alchornea*, 22μ (C-45,10; ESF G-46,4). — 19. *Brunellia*, 24μ (C-42,15; ESF U-31,1). — 20. *Abutilon*, 45μ (A-1,1; ESF H-36,1–2). — 21. *Faramea*, 32μ (C-46,6; ESF T-44,3). — 22. *Bombax*, 43μ (B-14; ESF O-17,2). — 23. *Bursera*, 29μ (B-17,5; ESF V-16,2. — 24–25. *Catostemma*, 33μ (C-43,1; ESF K-39,2). — 24. Outline.—25. Surface.—26. *Casearia*, 18 × 23μ (C-42,15; ESF S-36,4). — 27. *Chrysophyllum*, 13.5 × 18.9μ (C-41,1; ESF K-33,4). — 28–29. *Corynostylis*, 25μ (C-47,1; ESF P-22,2–4).—28. Outline.—29. Surface. — 30–31. *Dendropanax*, 25μ (C-46,15; ESF J-20,4).—30. Outline.—31. Surface. — 32. *Guarea*, 36μ (C-43,2; ESF U-42,1). — 33–34. *Fagus*, 39μ (A-1,1; ESF D-32,1).

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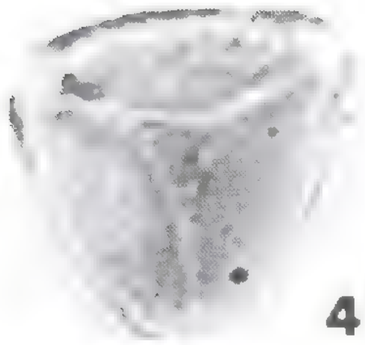

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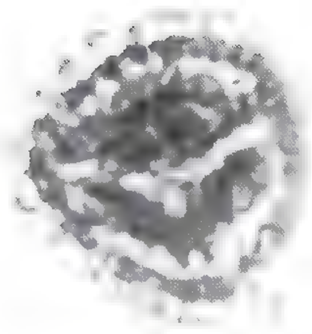

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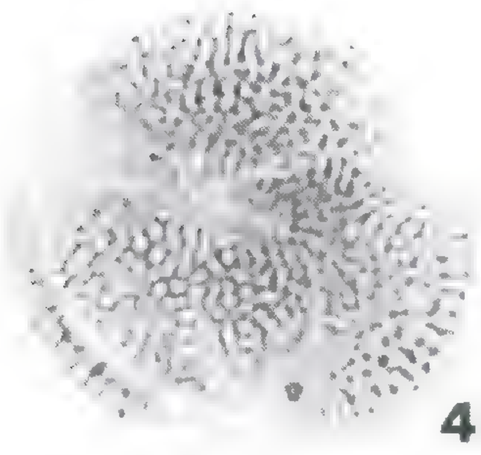

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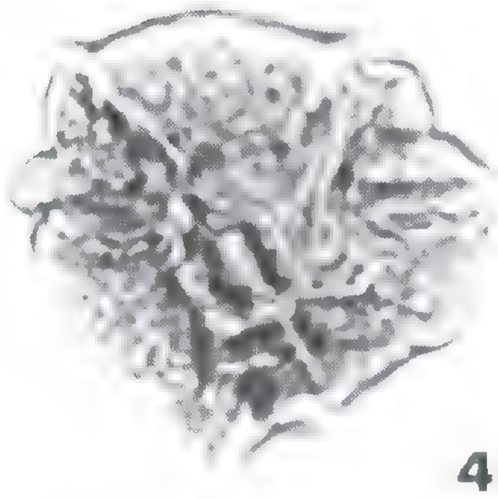

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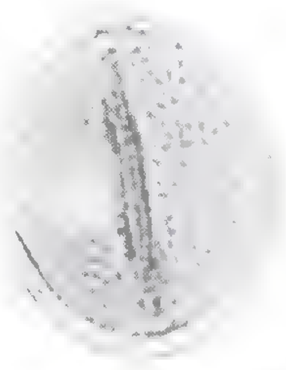

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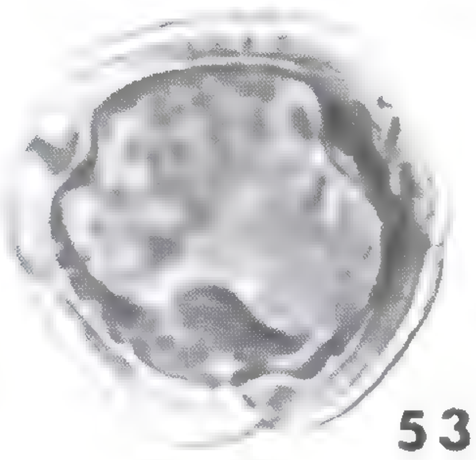

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pattern is somewhat different from other living counterparts of the microfossils, but there is some megafossil evidence that *A. incanum* may have had a wider distribution in the past. Hollick (1928) described fossil fruits from the Collazo Shales of Puerto Rico as *Malvocarpon clarum*. He states that ". . . generic relationship with *Abutilon* is strongly indicated by the shape and arrangement of the carpels" (p. 214) and compares the specimens to fruits of the modern *A. texense*, a synonym of *A. incanum* (*fide* Shreve & Wiggins, 1964: 880). Other reports of megafossils of *Abutilon* are Hollick (1936) from the Paleocene or Eocene of Alaska, and Berry (1925: 217), who described *Malvacarpus tertiarius* from Miocene deposits in Argentina and compared it to several modern genera including *Abutilon*.

Acacia (Fig. 14)

Acacia includes some 700 species distributed in warm-temperate regions; the largest concentrations are in Africa and Australia. The number of native species in regions with which the fossil assemblage has affinities is relatively few (*e.g.*, 1 species in Cuba, 17 species in northern Mexico; *fide* Shreve & Wiggins, 1964). The pollen of 60 species, including most of those from Latin America, were compared with the microfossils. The fossil is characterized by its exceptional size (72μ) and scabrate exine. These features are not common in modern species of *Acacia*, but are characteristic of *A. farnesiana*. This plant is a spiny shrub or small tree (3–4 m tall) of thickets and forests in the dry coastal limestone regions of Puerto Rico. Its geographic range is throughout Latin America and into southern Texas, California, and Arizona, and through cultivation along the Gulf States to Florida. It is considered to be introduced in the Antilles, although there is some debate about its natural occurrence in Cuba. The presence of *A. farnesiana* pollen in the San Sebastian microflora suggests it may be native to Cuba and other islands of the West Indies. Tsukada (1966) found *Acacia* polyads in Recent deposits from Guatemala, and Heusser (1966) reported *Acacia* from Late Pleistocene deposits in southern Chile. Megafossils identified as *Acacia* also occur in the Pliocene floras of Potosí, Bolivia (Berry, 1939: 45).

Aetanthus (Fig. 17)

The genus *Aetanthus* (Loranthaceae) is presently restricted to the northern Andes. There are about 15 species which grow in temperate forests at elevations of about 2,000 m. A single specimen was recovered from sample C-46. The genus has not previously been reported from the fossil record.

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FIGURES 37–53.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 37. *Hauya*, 85μ (C-42,9; ESF P-23,2).—38. *Jacaranda*, 50μ (C-46,8; ESF J-37,2). — 39–40. *Marcgravia*, 19μ (C-42,15; ESF R-29,4).—39. Outline.—40. Surface. — 41. *Eugenia*, 27μ (C-45,3; ESF L-19). — 42. *Ilex*, 25μ (C-47,15; ESF H-19). — 43–44. *Nyssa*, 50μ (C-41,1; ESF D-37,4.—43. Outline.—44. Surface. — 45. *Oxalis*, 32μ (A-12,1; ESF P-32,1). — 46. *Rauwolfia*, 35μ (B-39,1; ESF C-45,4). — 47–48. *Zanthoxylum*, 13 × 18μ (C-50,15; ESF N-26).—47. Outline.—48. Surface. — 49. *Pleodendron*, 23μ (C-41,6; ESF E-24,4). — 50. *Engelhardia*, 27μ (C-44,1; ESF U-24,3). — 51–52. *Liquidambar*, 35μ (C-43,1; ESF V-37,3).—51. Outline.—52. Surface. — 53. *Norantea*, 33μ (C-50,15; ESF N-30,4).

Alchornea (Fig. 18, 35–36)

Members of the genus *Alchornea* (Euphorbiaceae) are pantropical. There are about 70 widely distributed species (Fig. 71), represented in the New World tropics by a well-circumscribed section, *Alchornea*. Forty species occur in South America where they are common members of hydrosere successions along river banks and swamps. Species from Mexico and Central America are fewer in number and commonly grow in rain forests, wet lowlands, and rocky montane areas.

A single species, *A. latifolia*, grows in Puerto Rico today (Little & Wadsworth, 1964: 262). It is a medium-sized, rapid-growing evergreen tree attaining heights of 10–20 m. The trees are most common in the montane rain forests (*e.g.*, Cerro de Punta), but they also occur in moist limestone coastal regions, growing mainly in openings and along roadsides. This species also occurs on Cuba, Jamaica, Haiti (*A. haitiensis* also present), and Tortola; and from Veracruz, Mexico, south to western Panama (G. L. Webster, personal communication, 1969).

Microfossils of *Alchornea* are common in the San Sebastian Formation, occurring in nearly every sample (0.5–1.0%). They also occur in Pleistocene deposits from El Salvador and Guatemala (Tsukada & Deevey, 1967), Upper Cretaceous-Tertiary of Guyana (Hammen & Wijmstra, 1964, as *Psilatricolporites operculatus*), in the Lower and Middle Eocene of Tibu, Colombia (Gonzalez-Guzman, 1967), and in our Miocene samples from the Paraje Solo Formation, Veracruz, Mexico.

Bernoullia (Fig. 15)

There are two species of *Bernoullia* (Bombacaceae) distributed from southern Mexico through Central America into the tropical regions of northern South America (Fig. 72). These are large trees (30 m tall) and are deciduous during the latter part of the dry season. Microfossils are common at Locality C with an abundance as high as 2.5%. There are no other reports of the genus in the fossil record.

Bombax (Fig. 22)

Members of *Bombax* are tropical and include about eight species in Mexico, Central and South America. The plants are common in damp tropical forests.

Microfossils of *Bombax* are rare in the Puerto Rican samples, with a single specimen recovered from Locality B-14 and B-24. Previous reports include Hammen (1954, as *Bombacacidites annae*) from the Lower Tertiary of Colombia, Norem (1955) from the Eocene of Venezuela, and Hammen (1963) from Quaternary deposits in Guyana. Tsukada (1966) also reports *Bombax* from Recent core material of Lake Petenxil, Guatemala.

Brunellia (Fig. 19)

The genus *Brunellia* (Brunelliaceae) consist of 45 species distributed in the Neotropics from Mexico through Central America to Peru. It is represented in Puerto Rico by *B. comocladifolia*, a medium-size evergreen tree (5–10 m tall) of the montane forests to elevations of 1,500 m or higher (Little & Wadsworth,

1964). The range of *B. comocladifolia* is throughout the Greater Antilles, Guadeloupe, and Venezuela and Colombia.

Microfossils were recovered from samples C-43 and C-48 (1.0–1.5%). The fossils are similar to several modern species of *Brunellia,* including *B. comocladifolia.* The genus has not previously been reported from the fossil record.

Bursera (Fig. 23)

The genus *Bursera* (Burseraceae) is warm-temperate to tropical in distribution, consists of about 100 species, and occurs throughout Mexico, Central America, the Antilles, and northern South America (Brizicky, 1962*a*). The western Mexican species have recently been monographed by McVaugh and Rzedowski (1965). The most widespread species is probably *B. simaruba* which grows through the entire range of the genus (Little & Wadsworth, 1964). In Puerto Rico this species is a medium-size deciduous tree 20–40 feet tall and is common in deciduous forests with soils derived from limestone.

A single pollen grain was recovered from sample B-17. It is similar to a number of modern species including *B. simaruba.* Pollen of *Bursera* is also known from Recent core sediments from Lake Petenxil in northern Guatemala, Tsukada, 1966). Megafossils of *Bursera* are reported from the Lower Oligocene Florissant beds of Colorado (MacGinitie, 1953; *cf.* McVaugh & Rzedowski, 1965: 318).

Casearia (Fig. 26)

Casearia (Flacourtiaceae), with about 160 species, is pantropical in distribution. Some 40 species occur in Mexico and Central America; 90–100 grow in South America and about 25 in the West Indies (Fig. 73). At least seven species are native to Puerto Rico; *C. arborea, C. aculeata, C. bicolor, C. decandra, C. guianensis, C. ramiflora,* and *C. sylvestris.* In Puerto Rico the genus is widely distributed along roadsides, thickets, and in the lower montane moist limestone and moist coastal regions. It is a small evergreen tree (10 m tall), which invades the understory of moist tropical forests.

Pollen of *Casearia* occurs only in samples C-42 and C-47, with an abundance of less than 0.5%. Hammen and Wijmstra (1964) illustrate pollen similar to *Casearia* from the Tertiary of Guyana as *Psilatricolporites cyamus.* Berry (1938: 106–107) reported leaf material from the Lower Miocene of Río Pichileufu, Argentina, as similar to the modern *C. arguta.* In the same paper Berry states that the only previous report was that of Engelhardt from the Lower Miocene of Chile.

Catostemma (Fig. 24–25)

The genus *Catostemma* (Bombacaceae) is a New World group of six species ditributed in Guyana, Venezuela, and Brazil. The trees are most abundant in the tropical rainforests of Guyana where the average annual rainfall is over 250 cm. Here they reach heights of 30 m and are codominants in the canopy layer along with *Mora* and *Eschweilera* (Richards, 1966: 238–239).

Pollen of the six species of *Catostemma* can be separated into two groups. One type (four species) is 4–6 stephanocolpate with a densely and evenly perforated tectum. The second type is 4–6 stephanoporate and echinate; *C. praecox*

and *C. micranthum* are included here. The microfossils are of the latter type. Presently *C. praecox* and *C. micranthum* are restricted to the rain forests of Brazil.

The abundance of *Catostemma* pollen in the San Sebastian Formation is 0.5% in sample A-12, and it is common at Locality C. Pollen has also been reported from the Upper Eocene to earliest Oligocene of Guyana and is cited as occurring into the Lower Miocene of the Caribbean area (Germeraad, *et al.*, 1968). According to these authors the pollen shows strong local abundance especially in the Oligocene and Lower Miocene. Other reports of fossil pollen of *Catostemma* are those of Hammen (1963) from the Quaternary of Guyana and probably that of Norem (1955) from the Upper Eocene of Venezuela, listed as "tetracolpate pollen." The presence of *Catostemma* pollen in the Puerto Rican samples considerably extends the known geographic range of the genus during Tertiary times.

Chrysophyllum (Fig. 27)

This large genus of Sapotaceae is distributed throughout the tropical regions of the world. It is especially common in the American tropics (Fig. 74). Species in the New World are found in the moist wooded and montane forests of Mexico, Central America, and throughout the West Indies; one species, *C. oliviforme* occurs in southern Florida (Wood & Channell, 1960).

Three species are common to Puerto Rico and adjacent islands—*C. argenteum*, *C. cainito*, and *C. oliviforme*. These are evergreen shrubs or trees reaching heights up to 15 m (Little & Wadsworth, 1964). The trees are common in the moist limestone and lower montane forests, primarily in northern and western Puerto Rico.

Microfossils of *Chrysophyllum* are present in samples B-25 (0.5%) and C-41 and C-47 as single specimens. The pollen of *Chrysophyllum* is similar to some members of the Burseraceae, although pollen of the Burseraceae is usually about 50% larger. Hollick (1928) described two species and one variety of megafossils of *Chrysophyllum* from the Collazo River area. He compared this material to *C. argenteum* and *C. cainito*. Other reports of megafossils are Berry (1939: 154) from the Pliocene of Venezuela, and Berry (1938: 45) from the Eocene of Venezuela.

Corynostylis (Fig. 28–29)

The genus *Corynostylis* (Violaceae) consists of only four species, distributed from Veracruz, Mexico, into South America (Fig. 75). The most wide-ranging species, *C. arborea*, is a woody vine reaching tree girth. It is common along river banks in tropical forests. This species grows throughout the range of the genus, while the others are restricted to Brazil, Colombia, and Peru.

Microfossils of *Corynostylis* occur in samples B-19, C-43, C-47, and C-50 with an abundance of 0.5%. There are no other reports of *Corynostylis* in the fossil record.

Dendropanax (Fig. 30–31)

The genus *Dendropanax* (Araliaceae) occurs in tropical and subtropical regions throughout the world and includes about 75 species. The American species (about 45) occur in Mexico as far north as the state of Tamaulipas, throughout

Central America, and into South America (Fig. 76). *Dendropanax* is common in montane forests and mainly consists of trees with a few shrubs. A medium-size evergreen tree reaching heights of 15 m or more, *D. arboreus* is common in Puerto Rico. It grows in the lower montane and moist limestone regions of Puerto Rico and is common in the coffee plantations of the Central and Western Cordilleras. Another species, *D. laurifolia,* also grows in Puerto Rico but is not as common.

The fossil pollen is rare, being recovered only from sample C-48 (0.5%). The only other fossil record of *Dendropanax* is by Dilcher and Dolph (1970), who reported leaves in Eocene deposits of western Tennessee.

Engelhardia (Fig. 50)

At present there are four species recognized in *Engelhardia*—*E. pterocarya* from Costa Rica; *E. mexicana* from Mexico, Guatemala, and Costa Rica; *E. nicaraguensis* from Nicaragua; and *E. guatemalensis* from Guatemala. According to D. E. Stone these can be reduced to two, *E. pterocarya* and *E. mexicana,* the latter with three subspecies (*cf.* also Manning, 1959). The genus has a discontinuous distribution along the cordillera from Orizaba, Mexico, to Boquete, Panama, and one collection is known from Colombia. *Engelhardia* is not known from the West Indies. These medium-size trees commonly grow at elevations of 1,000–1,500 m in wet mountains.

Fossil pollen of *Engelhardia* occurs at all localities, and at Locality C it constitutes 30–50% of the samples. Other reports include those of Traverse (1955) from the Oligocene (?) Brandon Lignite of Vermont; Wodehouse (1933) from the Eocene Green River Formation of Colorado and Utah; and Langenheim *et al.* (1968) from Oligo-Miocene deposits in Chiapas, Mexico. It is common in the Paraje Solo (Miocene) Formation of Veracruz, Mexico. Pollen of the genus is also recorded in several presently unpublished theses and manuscripts on Mississippi Embayment and British Columbia deposits. If all these reports are valid, *Engelhardia* formerly had an extensive geographic range and probably broader ecological tolerances. Reported megafossils are common in Tertiary deposits of the western United States (LaMotte, 1952).

Eugenia (Fig. 41)

The genus *Eugenia* (Myrtaceae) contains several hundred species—500 according to Wilson (1960). McVaugh (1963) states that as many as 2500 names have been referred to *Eugenia.* It is widely distributed throughout tropical and subtropical regions. About 150 species occur in Mexico and Central America, and at least 135 are found in South America, concentrated in Brazil. Eighty or more are reported from the West Indies, and at least 25 are found in Puerto Rico (Fig. 77; Little & Wadsworth, 1964). Among the common species are *E. aeruginea, E. rhombea,* and *E. stahlii,* which are small, erect evergreen trees (10–20 m tall) found in the montane forests at elevations up to about 1,000 m.

Microfossils of *Eugenia* are recorded from Locality C (0.5%). Other reports are Hammen and Gonzalez (1960) from Pleistocene-Holocene deposits in Colombia, Hammen (1962) from Recent sediments of Laguna de Los Bobos, Colombia, and Tsukada (1966) from Recent core samples of Lake Petenxil, Guatemala.

Megafossils of *Eugenia* have been reported by Hollick (1928) from the Oligocene of Puerto Rico, Berry (1929) from the Loja Basin (Late Miocene) of Ecuador, Berry (1937: 59) from the Uppermost Miocene of Trinidad, and Berry (1939: 126, 151) from the Miocene of Cuba and the Mio-Pliocene of Venezuela.

Fagus (Fig. 34–35)

Fagus, with about ten species, is mostly north temperate in distribution with one species, *F. mexicana,* reported from Zacualtipan, Hidalgo, Mexico, at an elevation of 1,800 m. An account of the distribution of *Fagus* in Mexico is given by Fox and Sharp (1954).

Fossils are present in sample A-3 with an abundance of 1.0%. Pollen of six species was compared to the microfossil, and it is most similar to *F. americana.*

Faramea (Fig. 21)

The genus *Faramea* (Rubiaceae) contains about 180 species of trees and shrubs which are widely distributed in Latin America (Fig. 78). Among these *F. occidentalis* is common in Puerto Rico. It is a shrub or small evergreen tree (3–10 m tall) and is common in the understory of moist limestone and lower montane regions.

The pollen of *Faramea* is dimorphic (Willis, 1966: 444), with 2- and 3-porate grains. The pollen of *F. occidentalis* is typically 3-porate, as is the microfossil. The pollen is present in samples B-25 (1.5%) and C-41 (less than 0.5%). The genus has not previously been reported in the fossil record.

Guarea (Fig. 32)

This genus of Meliaceae consists of about 150 species in Latin America (Fig. 79) and some 20 species in Africa. In Puerto Rico they are shrubs (*ca.* 2–3 m tall) to large evergreen trees (15–25 m tall) common in the moist forests of the lower montane limestone and moist coastal regions. Species in Puerto Rico include *G. guara, G. humilis, G. ramiflora,* and *G. trichilioides. Guarea ramiflora* along with *Lucuma multiflora* comprise the Maricao forests. The crown layer of this forest is mainly *G. ramiflora* and the ground cover is primarily seedlings of this species (Gleason & Cook, 1926).

Microfossils were recovered from Localities B and C (0.5%). Hollick (1928) reported *G. opinabilis* from the Oligocene of Puerto Rico, and Hollick and Berry (1924) described leaves of the genus from the Late Tertiary of Brazil and referred them to the modern *G. trichilioides.* Graham (1962*b*) transferred fruits described as *Ficus ceratops* from Upper Cretaceous beds of Wyoming to *Guarea.*

Hauya (Fig. 37)

Hauya consists of three species, *H. heydeana* (Chiapas, Mexico, and Guatemala), *H. microcerata* (Chiapas south to Honduras and El Salvador), and *H. elegans* (Hildago and San Luis Potosí, Mexico, south to Costa Rica). *Hauya glauca* is considered a subspecies of *H. microcerata* (Raven, personal communication, 1969). The pollen of other genera closely related to *Hauya* (*Calylophus, Clarkia,* and *Gaura*) was examined and found to be distinct from *Hauya.*

Ecologically *Hauya* occurs with oaks and other lush middle elevation vegetation. It does not range upward into the pine belt or downward into the seasonally drier deciduous vegetation. It is always rare, and phylogenetically is one of the most primitive genera of Onagraceae (Raven, personal communication, 1969).

During the Oligocene *Hauya* had a distribution considerably different than at present, and it grew in the West Indies where it no longer occurs. Microfossils were recovered from Locality C (less than 0.5%); there are no other reports of *Hauya* in the fossil record.

Ilex (Fig. 42)

The genus *Ilex* is widespread and includes about 400 species. At least 60 grow in Mexico, Central America, and the West Indies; and some 180 species occur in South America. These trees and shrubs occupy a wide variety of habitats from wet, tropical rain forests, pine forests, marshy thickets and swamps to mountain slopes. Four species are known from mountain slopes and wooded valleys of Puerto Rico—*I. macfadyenii, I. nitida, I. obcordata,* and *I. sintenisii.*

A single specimen was recovered from sample C-47. Previous reports from Latin America are those by Hammen and Gonzalez (1960) from Upper Pleistocene and Holocene deposits near Bogotá, Colombia, Hammen (1962) from Recent sediments (5,000 yrs.) of Laguna de los Bobos, Colombia, Hammen (1963) from the Quaternary of Guyana, and Tsukada (1966) from core material of Lake Petenxil, Guatemala.

Jacaranda (Fig. 38)

There are about 50 species of *Jacaranda* in Latin America (Fig. 80). The only species in Puerto Rico, *J. mimosifolia,* is introduced from Argentina (Little & Wadsworth, 1964). In its native habitat it is common in wet forests and on wooded hillsides.

The pollen of *Jacaranda* is similar to *Tecoma* (*cf.* Fig. 38, 58), but the former is considerably larger. The single microfossil is present in sample C-46. There are no other reports of the genus in the fossil record.

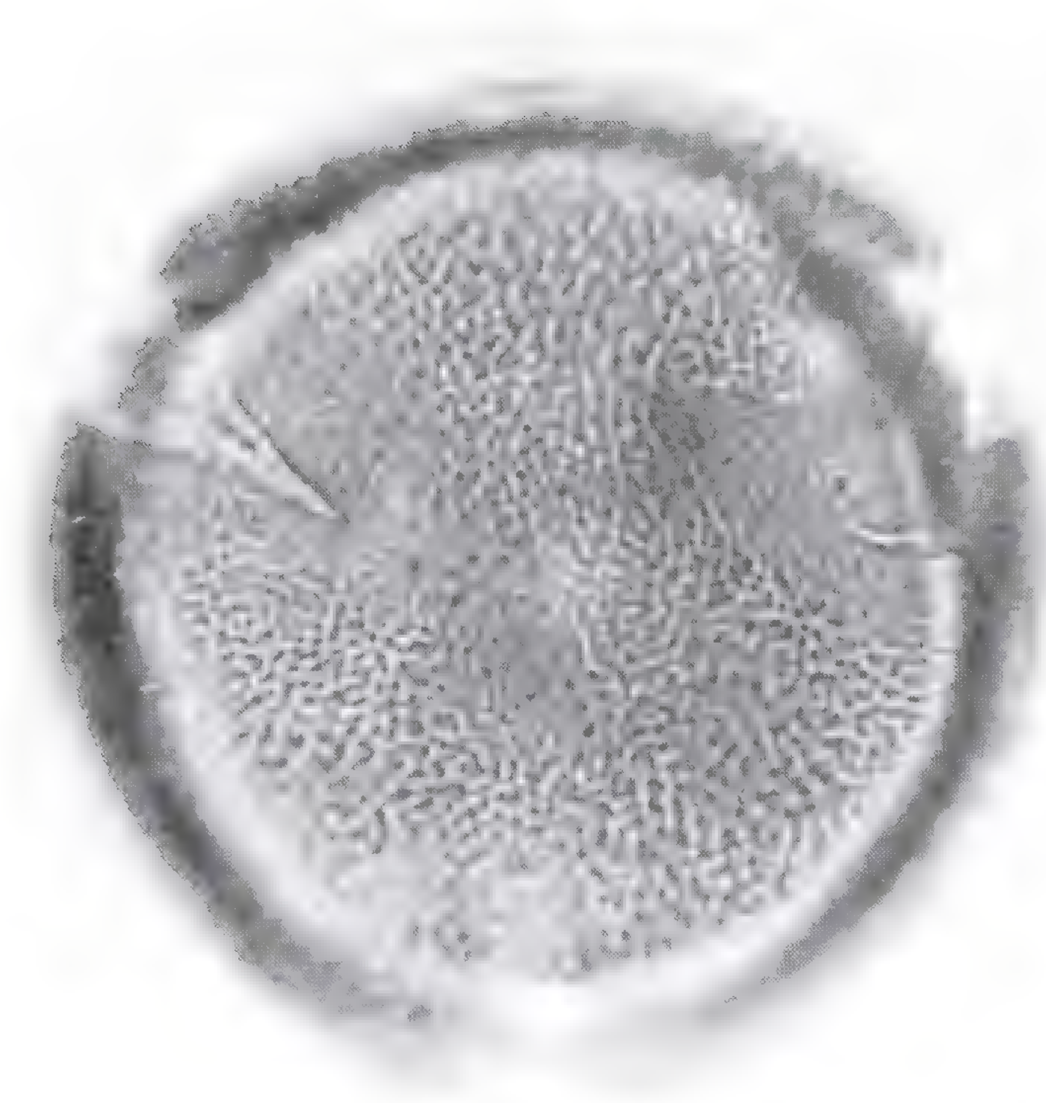
Liquidambar (Fig. 51–52)

There are three species of *Liquidambar* in the Atlantic States and Eastern Asia (Ernst, 1963). The species from the eastern United States, *L. styraciflua,* is common in deciduous forests along river flood plains and other mesic temperate habitats. It ranges into Mexico and Honduras (as *L. macrophylla* or *L. styraciflua* var. *mexicana*) and grows in the montane forests at elevations of 1,000–2,000 m.

Microfossils of *Liquidambar* are present at Locality C with an abundance of 0.5–2.0%. Tsukada (1966) has reported pollen from Recent core samples, Lake Petenxil, Guatemala. A review of the fossil history of the genus, based on pollen data, is given by Kuprianova (1960). There are numerous reports of megafossils (LaMotte, 1952).

Marcgravia (Fig. 39–40)

The genus *Marcgravia* (Marcgraviaceae) occurs in Central and South America and the West Indies (Fig. 81). There are about 55 species of these climbing,



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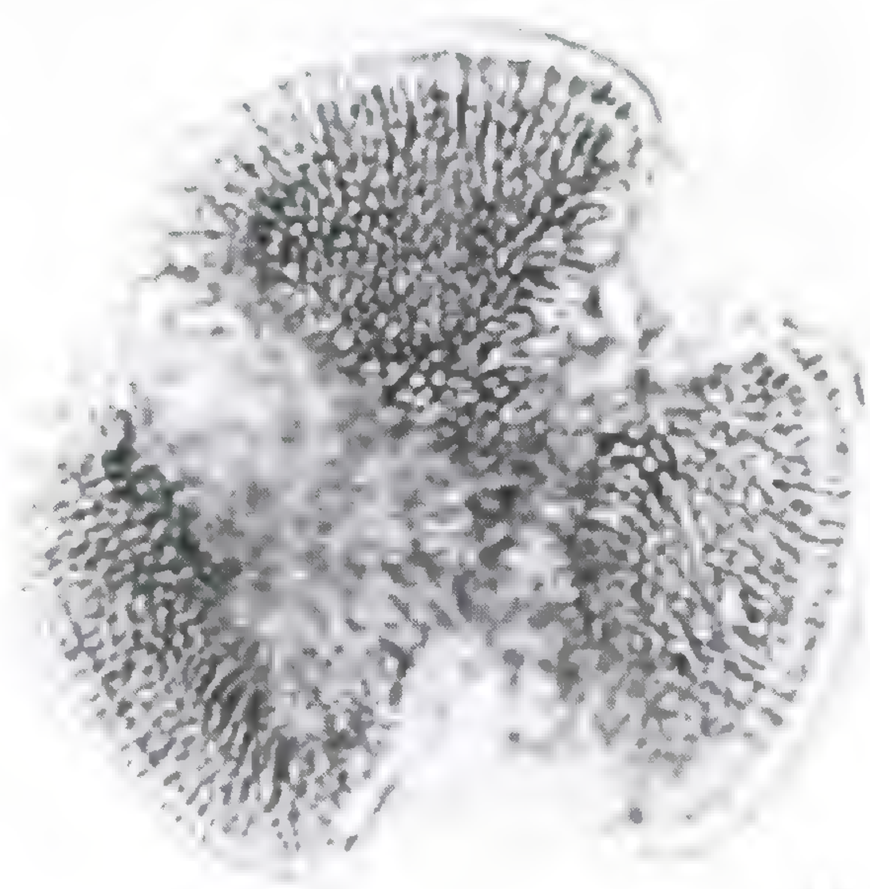

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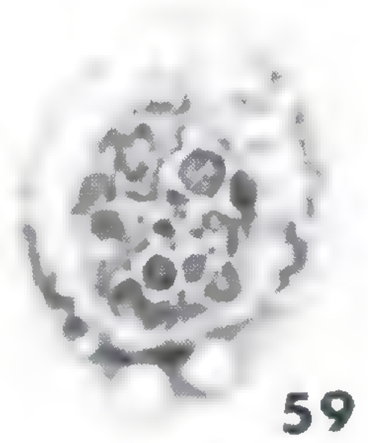

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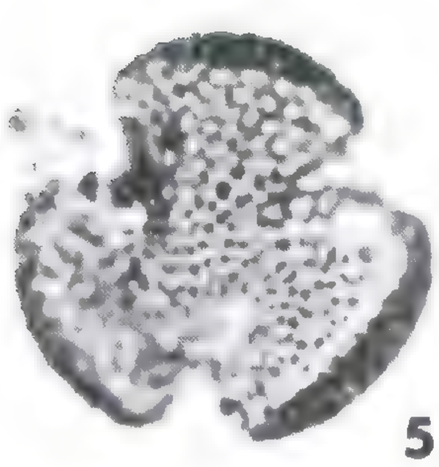

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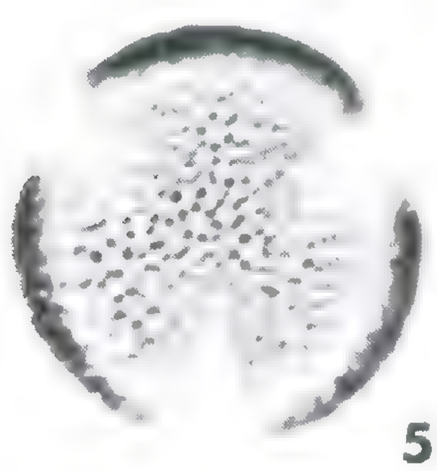

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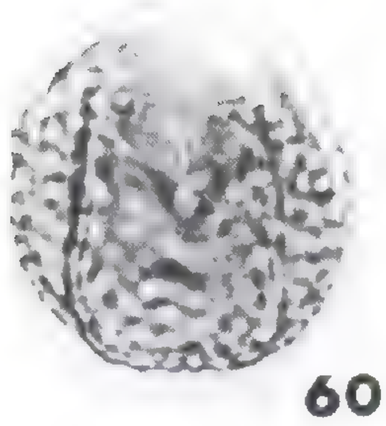

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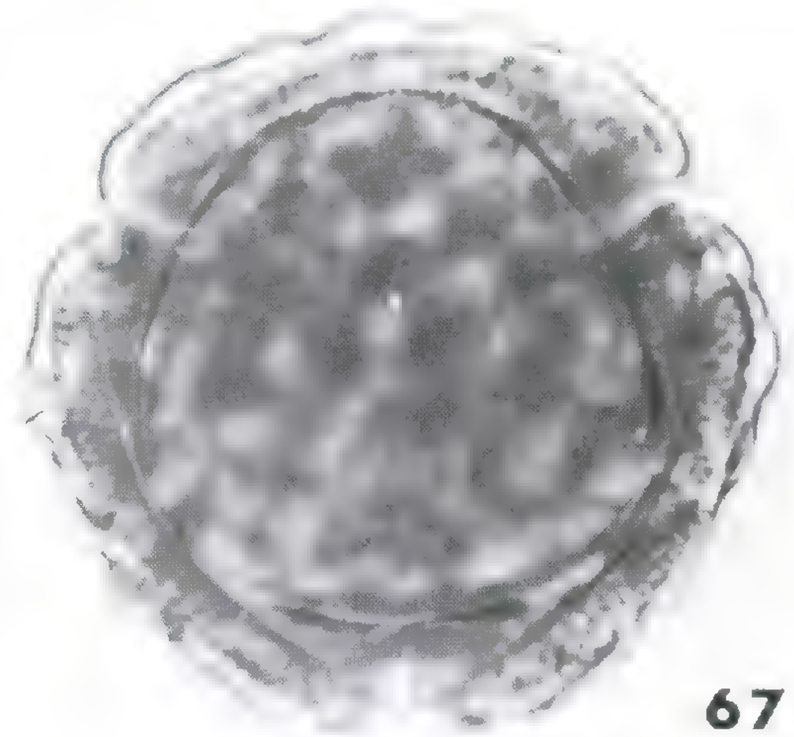

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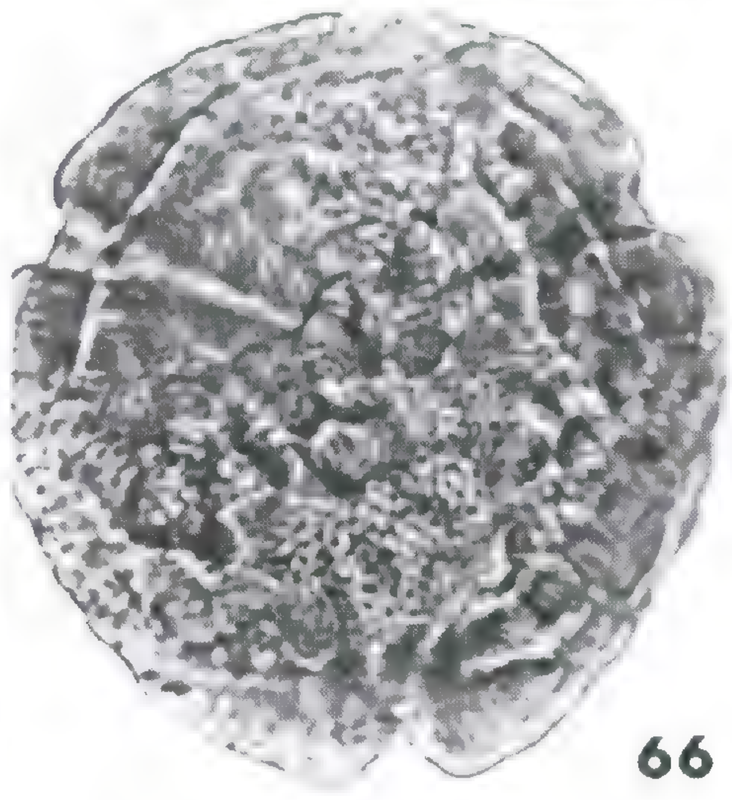

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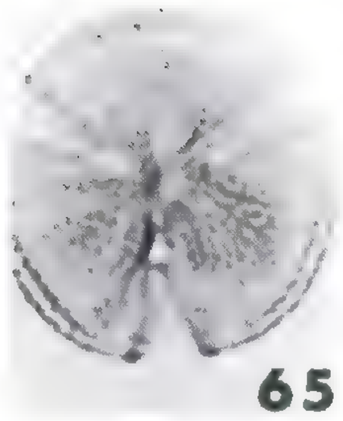

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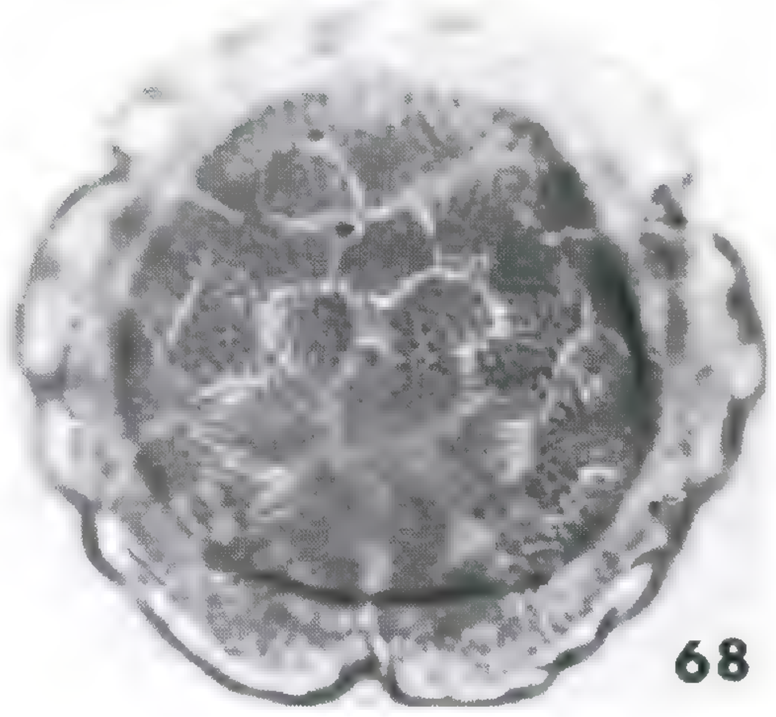

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epiphytic shrubs, including *M. sintenisii* and *M. rectiflora*. The latter is common in the rain forests of Puerto Rico and under favorable conditions the adult plant, 2–3 m in diameter, becomes a dominant feature of the forest.

A single pollen grain was recovered from sample C-42. Its infrequent occurrence is consistent with the small amount of pollen produced by the cleistogamous flowers of some species. The genus has not previously been reported from the fossil record.

Merremia (Fig. 55)

Merremia (Convolvulaceae) grows in warm temperate regions throughout the world (Willis, 1966). There are about 80 species, and 40 of these are found in the neotropics (Fig. 82). The plant is a herbaceous liana, commonly an early invader in secondary successions (Richards, 1966: 393). Eight species grow in the West Indies occupying open places, bluffs, and dry lowland habitats (*M. aegyptia, M. alata, M. cissoides, M. dissecta, M. quinquefolia, M. tridentata, M. tuberosa,* and *M. umbellata*).

The single microfossil specimen from sample C-42 was compared to pollen of species presently growing in the Antilles and is most similar to *M. dissecta*. Fossil pollen has also been reported by Gonzalez-Guzman (1967) from the Lower and Middle Eocene of the Tibu region in Colombia.

Myrica (Fig. 62)

The genus *Myrica* is almost cosmopolitan in distribution with 35 known species. There are about 17 species of these trees and shrubs widely distributed throughout Mexico, Central America, and the Antilles. An additional 15 or more are known from South America. Two common members of the Puerto Rican flora are *M. deflexa* and *M. splendens*. These are medium-size, evergreen trees (3–10 m tall), growing in the shaded understory of the lower montane forests on nearly all the islands of the Antilles.

A single microfossil was recovered from sample C-42. Previous reports of fossil pollen are those of Hammen and Gonzalez (1960) from the Upper Pleistocene and Holocene of Colombia, Hammen (1962) from Recent sediments (5,000 yrs.) from Laguna de Los Bobos, Colombia, and Tsukada (1966) from Lake Petenxil, Guatemala.

Norantea (Fig. 53)

The genus *Norantea* (Marcgraviaceae) includes about 35 species of the American tropics, being most abundant in South America (Fig. 83). They are lianas which superficially resemble *Philodendron* (Willis, 1966: 777).

←

FIGURES 54–68.—San Sebastian (Oligocene) microfossils, Puerto Rico. — 54, 66–68. ***Pelliciera*** **(C-48,1; ESF D-38,2).—54. 72μ.—66. 55μ.—67. Outline, 54μ.—68. Surface, 54μ.** — 55. *Merremia,* 63μ (C-42,9; ESF P-41,3). — 56–57. *Tetrorchidium,* 32μ, (B-14,10; ESF M-22,1).—56. Low focus.—57. High focus. — 58. *Tecoma,* 27μ (C-48,1; ESF U-20,4). — 59. *Tournefortia,* 28μ (A-12,10; ESF U-34,4). — 60 61. *Salix,* 27μ (C-46,15; ESF L-30,3).—60. Outline.—61. Surface. — 62. *Myrica,* 20μ (C-42,4; ESF N-43). — 63–65. ***Rhizophora*** **(C-47,1; ESF L-21,3).—63. 14μ.—64. 24μ.—65. 28μ.**

A single specimen was recovered from sample C-50. There are no previous reports of *Norantea* from the fossil record.

Nyssa (Fig. 43–44)

Nyssa (Nyssaceae) consists of about five or six species distributed widely in the Himalayas, eastern Asia, western Malaysia, and eastern North America (Eyde, 1966). The eastern American species, *N. aquatica* and *N. sylvatica,* range from Maine, the Great Lakes, and southern Canada south to the Brazos River in Texas and Lake Okeechobee in Florida. The latter also occurs in the highlands of Hidalgo, Puebla, and Chiapas, Mexico, at elevations of 1,000–1,700 m. It is frequently associated with *Liquidambar, Quercus,* and *Pinus strobus.* Miranda (1945) has discussed the presence of *Nyssa* in Mexico.

Microfossils from the San Sebastian Formation are present at Localities A and C and are most common in sample C-48 (4.5%). The fossil record of *Nyssa* is extensive (Eyde, 1963; Eyde & Barghoorn, 1963); however, we know of no other records from northern Latin America.

Oxalis (Fig. 45)

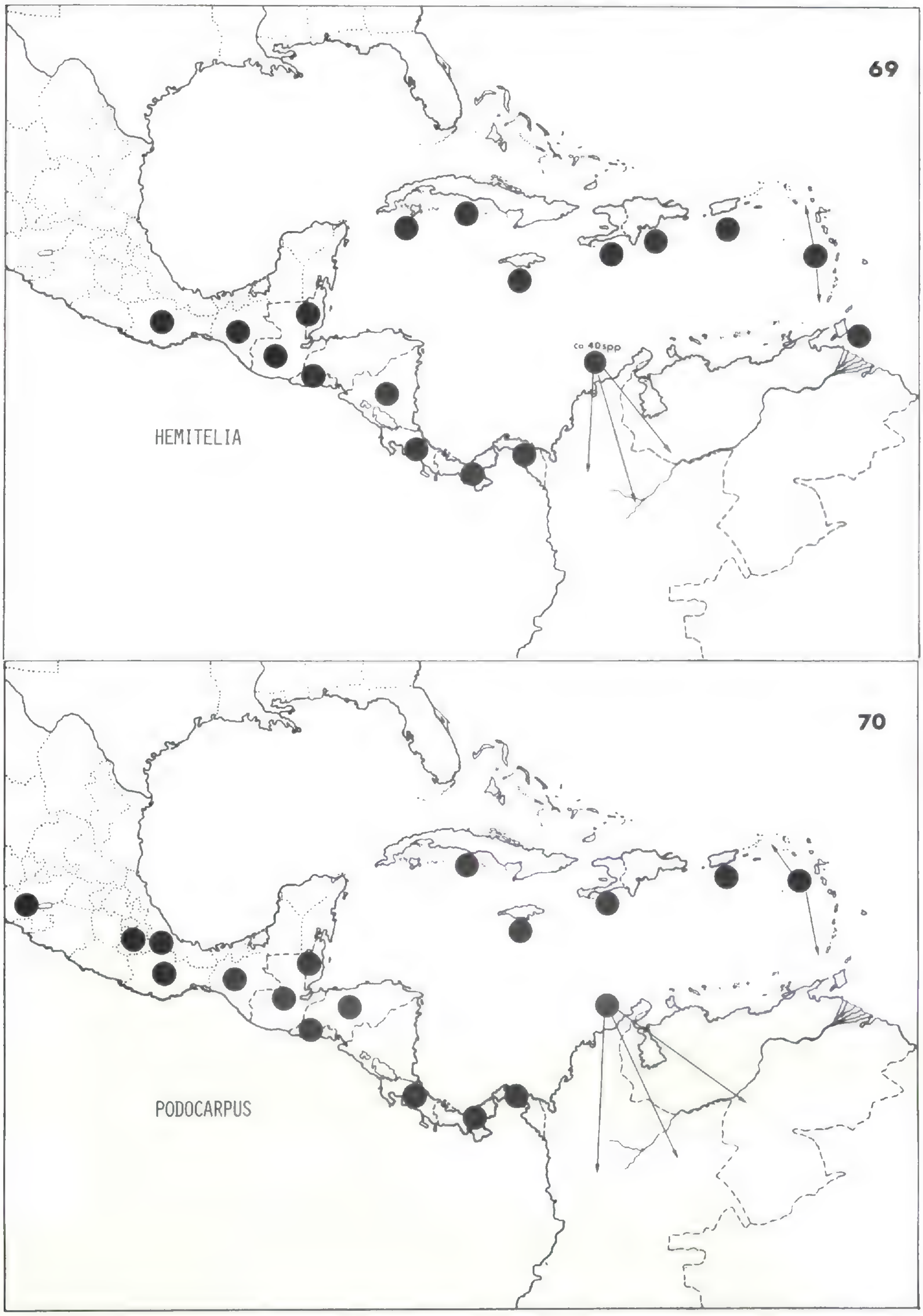
The genus *Oxalis* is widely distributed, consisting of about 800 species. It is particularly abundant in Central and South America. At least 20 species grow in the Antilles as small herbs of diverse habitats. Microfossils of *Oxalis* are rare occurring only in sample A-12 (less than 0.5%). There are no previous reports of the genus in Tertiary deposits of Latin America; Brown (1938) has reported *Oxalis* from the Pleistocene of Louisiana, the only other record known to us.

Pelliciera (Fig. 54, 66–68)

The genus *Pelliciera* (Theaceae; Pellicieriaceae *fide* Willis, 1966) is represented in the modern flora by a single species, *P. rhizophorae.* It is a small tree, 8–10 m tall, with buttress roots and a mangrove habit. It occurs along sandy beaches, swamps, and mud flats, frequently associated with other mangrove genera. The distribution of *Pelliciera* (Fig. 84) is from Costa Rica, south through Panama, and into northwestern South America (Colombia, Ecuador).

The present range of *Pelliciera* is considerably restricted when compared to its former occurrence. Wijmstra (1968) has reported pollen from Oligocene to Miocene beds of the Guiana Basin of northern South America. Wijmtsra also cites references to other occurrences in the Marago Basin of Brazil (Miocene) and from a Miocene pollen flora in Venezuela. Langenheim *et al.* (1967) have identified *Pelliciera* pollen from Oligo-Miocene beds in Chiapas, Mexico. It is also present in our samples of Middle Tertiary age in the Canal Zone, Panama. The fossil record of *Pelliciera* is from the Middle Oligocene to the Present, and these sites are distributed as far north as Chiapas, Mexico and Puerto Rico.

The pollen recovered shows considerable diversity in size and morphology. The grains range in size from 50–90μ and include coarsely scabrate to verrucate forms. The same variation is evident in pollen of the modern *P. rhizophorae.*



FIGURES 69–70.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—69. *Hemitelia*.—70. *Podocarpus*.

Pleodendron (Fig. 49)

The genus *Pleodendron* (Canellaceae) with two species is restricted to the West Indies. *Pleodendron ekmanii* is known only from wooded hillsides in Haiti at elevations of 800 m, and *P. micranthum,* a tall tree of virgin forests, occurs in the Sierra de Luquillo, Puerto Rico, at elevations of about 1,200 m. Microfossils of *Pleodendron* are present in samples C-41, 43, and 50 (0.5%). There are no other fossil records of the genus.

Rauwolfia (Fig. 46)

Rauwolfia (Apocynaceae) consists of about 100 species distributed throughout tropical regions of the world. There are 15–20 species in Mexico and Central America, about 40 species in South America, and 10–15 from the Antilles. In Puerto Rico the genus is represented by *R. nitida,* a small tree or shrub (7–14 m tall), and *R. viridius,* a shrub about 1–4 m tall (Fig. 85). The plants grow in the coastal and limestone forests and thickets, usually in open habitats.

A single specimen was recovered from sample B-39. There are no other fossil records.

Rhizophora (Fig. 63–65)

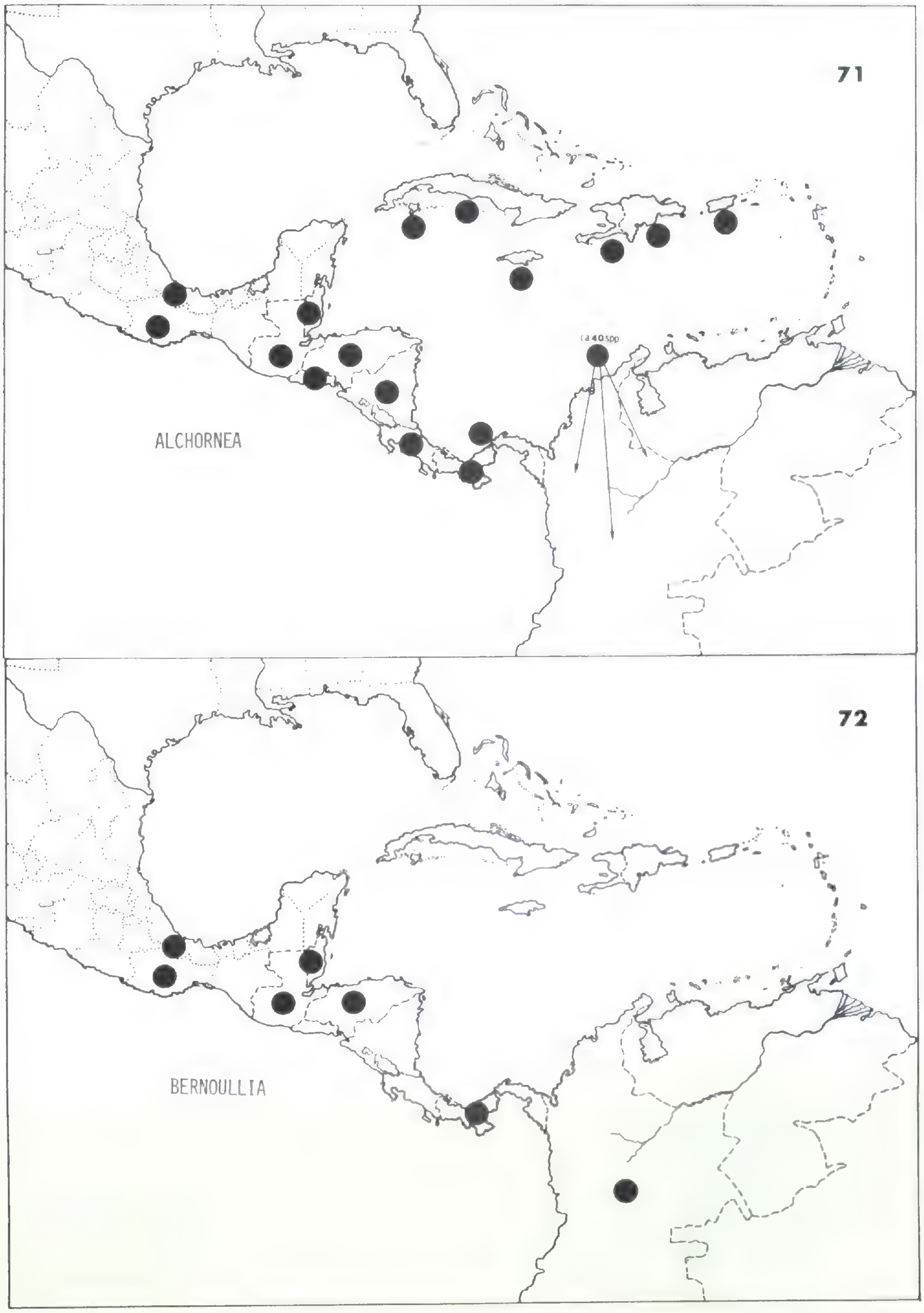
The genus *Rhizophora* contains 6–9 species distributed throughout the world along tropical coasts. The plants are gregarious trees or shrubs inhabiting mud flats of coastal tidal marshes, brackish streams and lagoons (S. Graham, 1964). Two species grow in areas with which the microflora has affinities—*R. racemosa,* infrequent in the Americas but more common along the African shore, and *R. mangle* which ranges from southern Florida to northern South America.

The pollen recovered includes as extremes a small, psilate type with distinct colpi transversales and a larger form with a scabrate surface pattern and less distinct colpi transversales. According to Langenheim *et al.* (1967) these variations are included within the pollen of *R. mangle.*

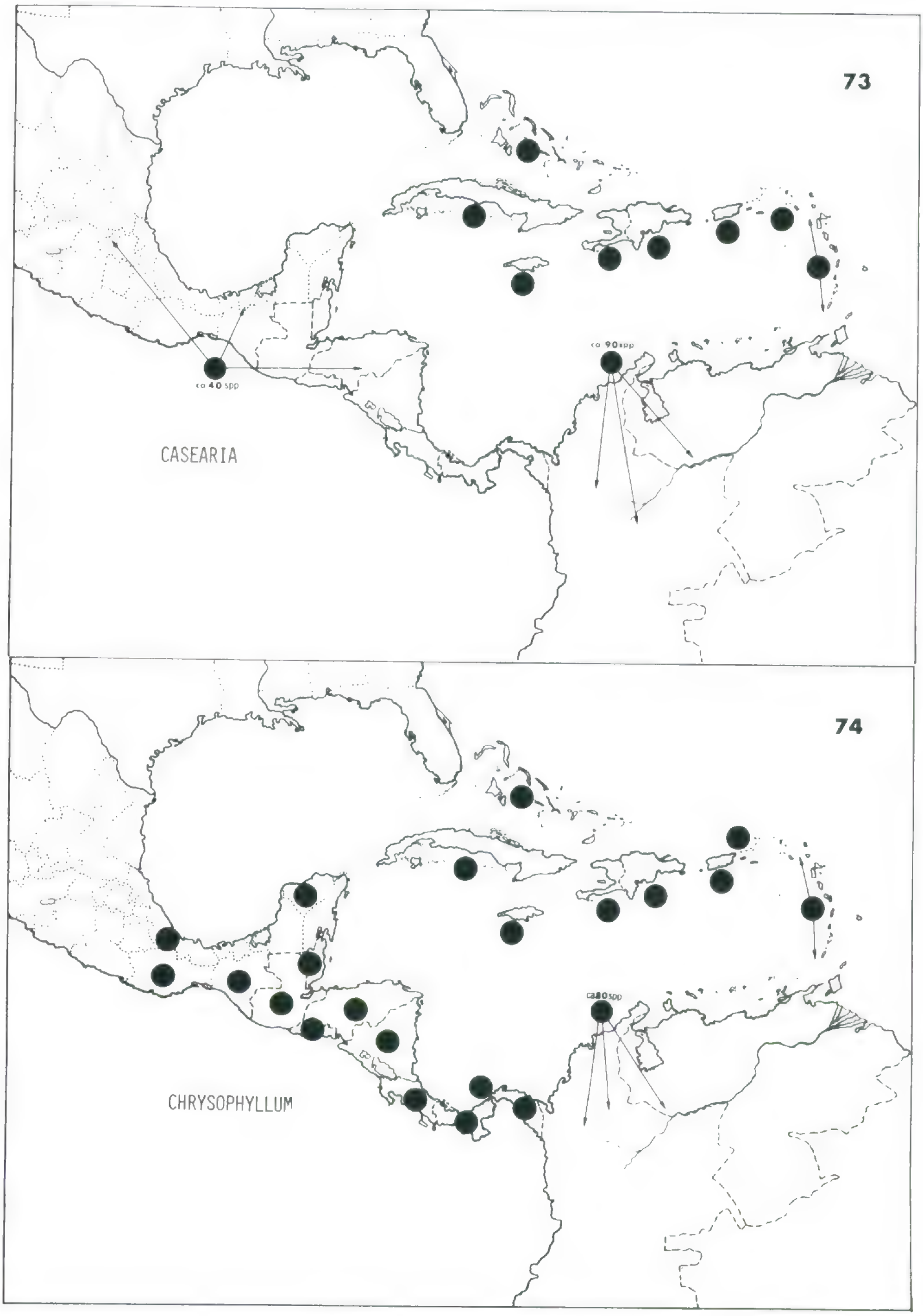
Fossil pollen of *Rhizophora* is found at all localities with an abundance of 96% at Locality A, 77% at Locality B, and 1–2% at Locality C. Latin American records of the genus are common and include those of Hammen (1963) from the Quaternary of Guayana and Langenheim *et al.* (1967) from the Oligo-Miocene of Chiapas, Mexico. It is also present in our samples from the Miocene of Veracruz, Mexico, and the Middle Tertiary (Oligo-Miocene to Middle Miocene) of Panama. Hollick (1928) records megafossils from the Oligocene of Puerto Rico.

Salix (Fig. 60–61)

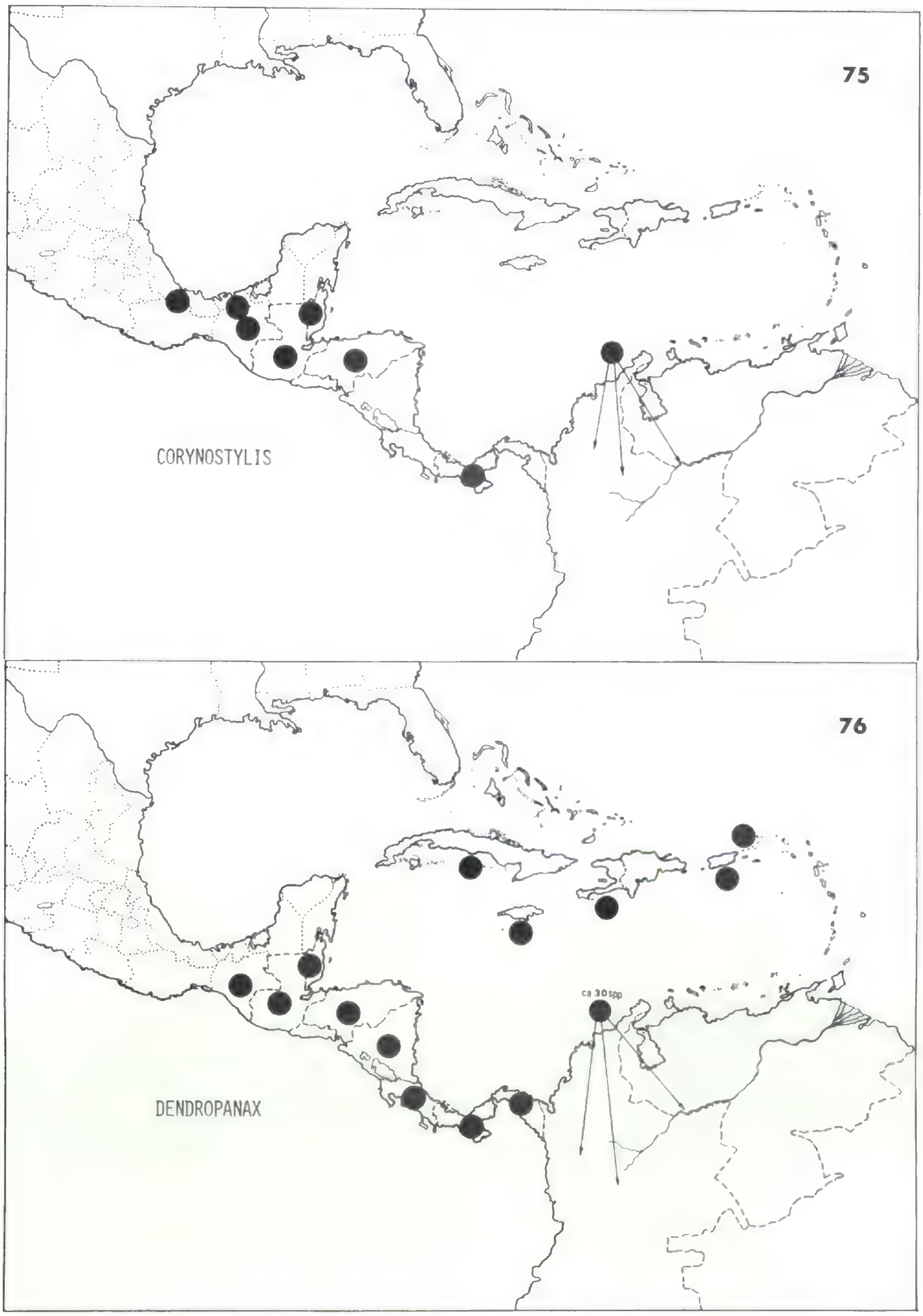
The genus *Salix* includes about 500 species, chiefly north temperate in distribution, but with at least 15 species occurring in Mexico, Central America, and the Antilles. An additional ten species are known from South America. Species of *Salix* range from trees to shrubs and subshrubs, and although most common in moist, mesic environments, they occupy a wide range of habitats. Microfossils were recovered from samples C-43 (1%), C-46 (0.5%), and C-48 (0.5%). We know of no other reports of the genus from Latin American deposits.



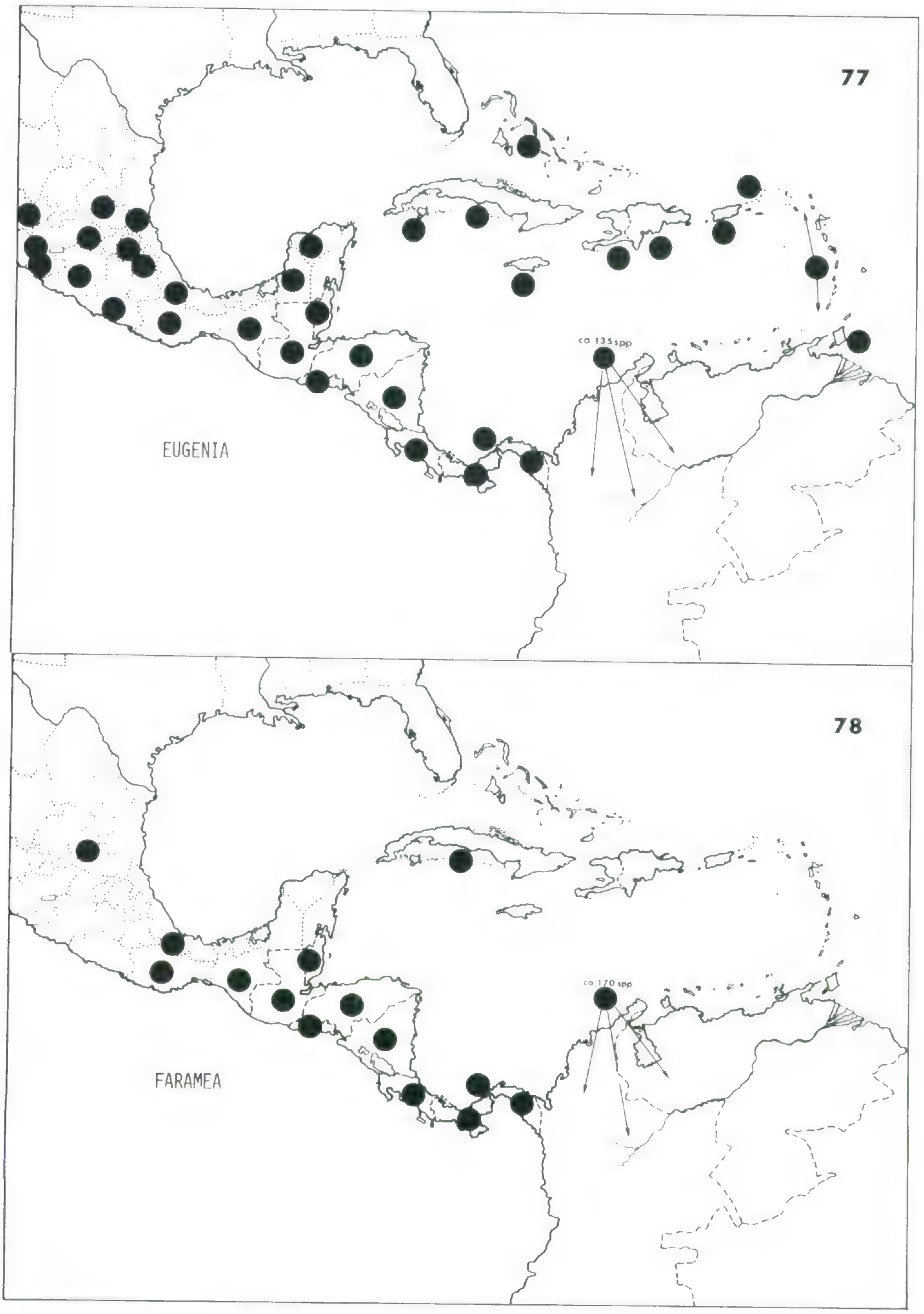
FIGURES 71–72.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—71. *Alchornea*.—72. *Bernoullia*.



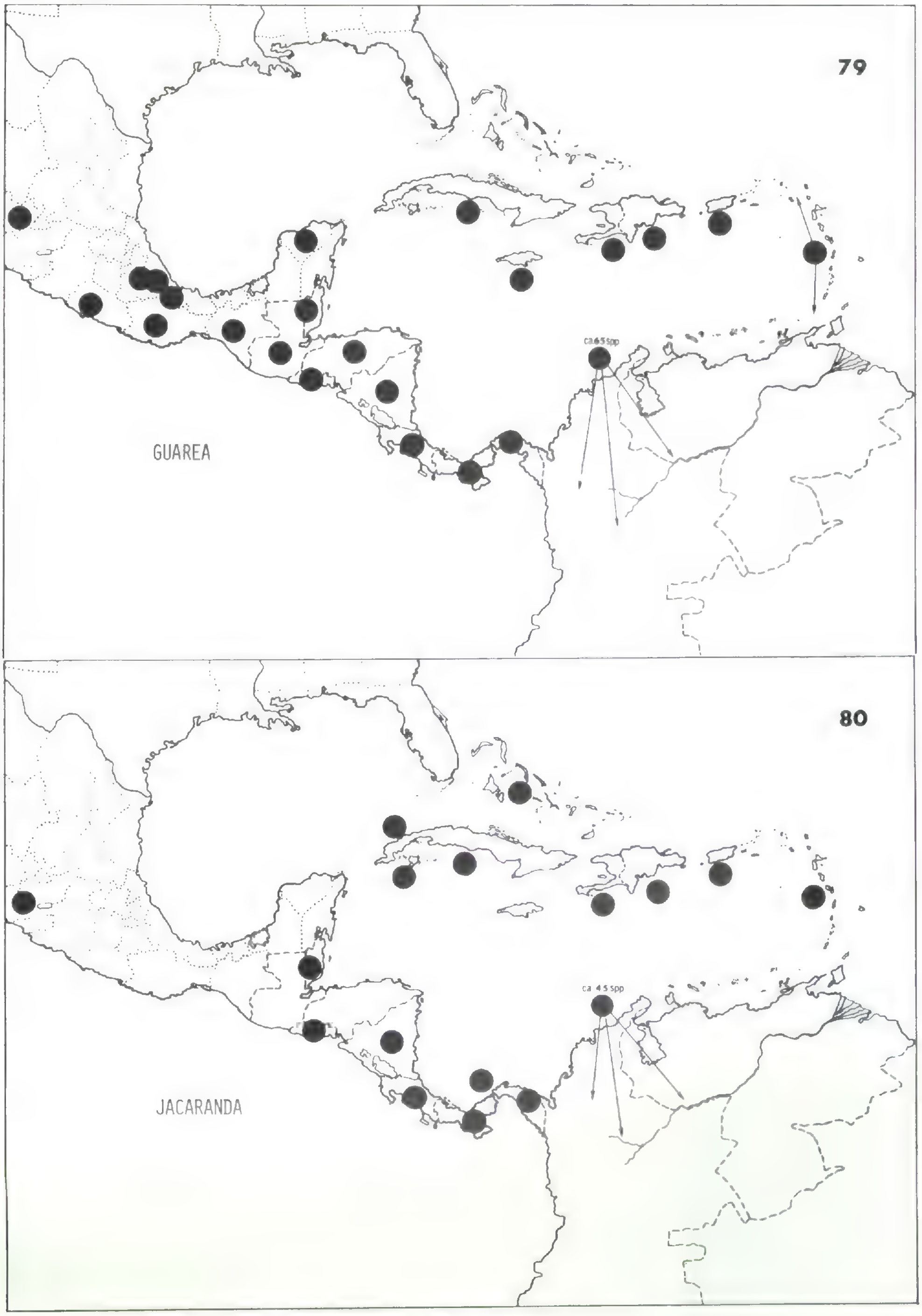
FIGURES 73–74.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—73. *Casearia*.—74. *Chrysophyllum*.



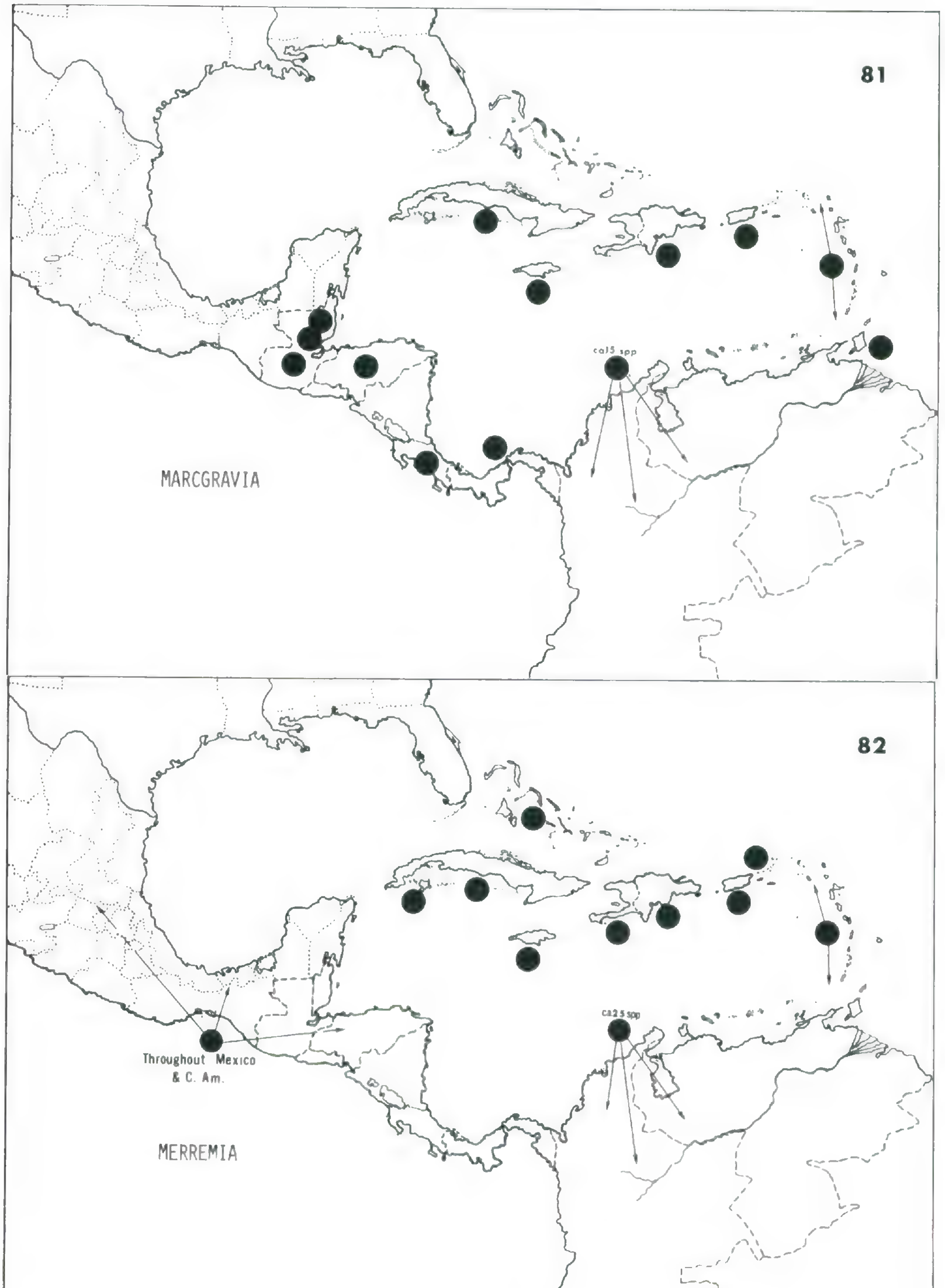
FIGURES 75–76.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—75. *Corynostylis*.—76. *Dendropanax*.



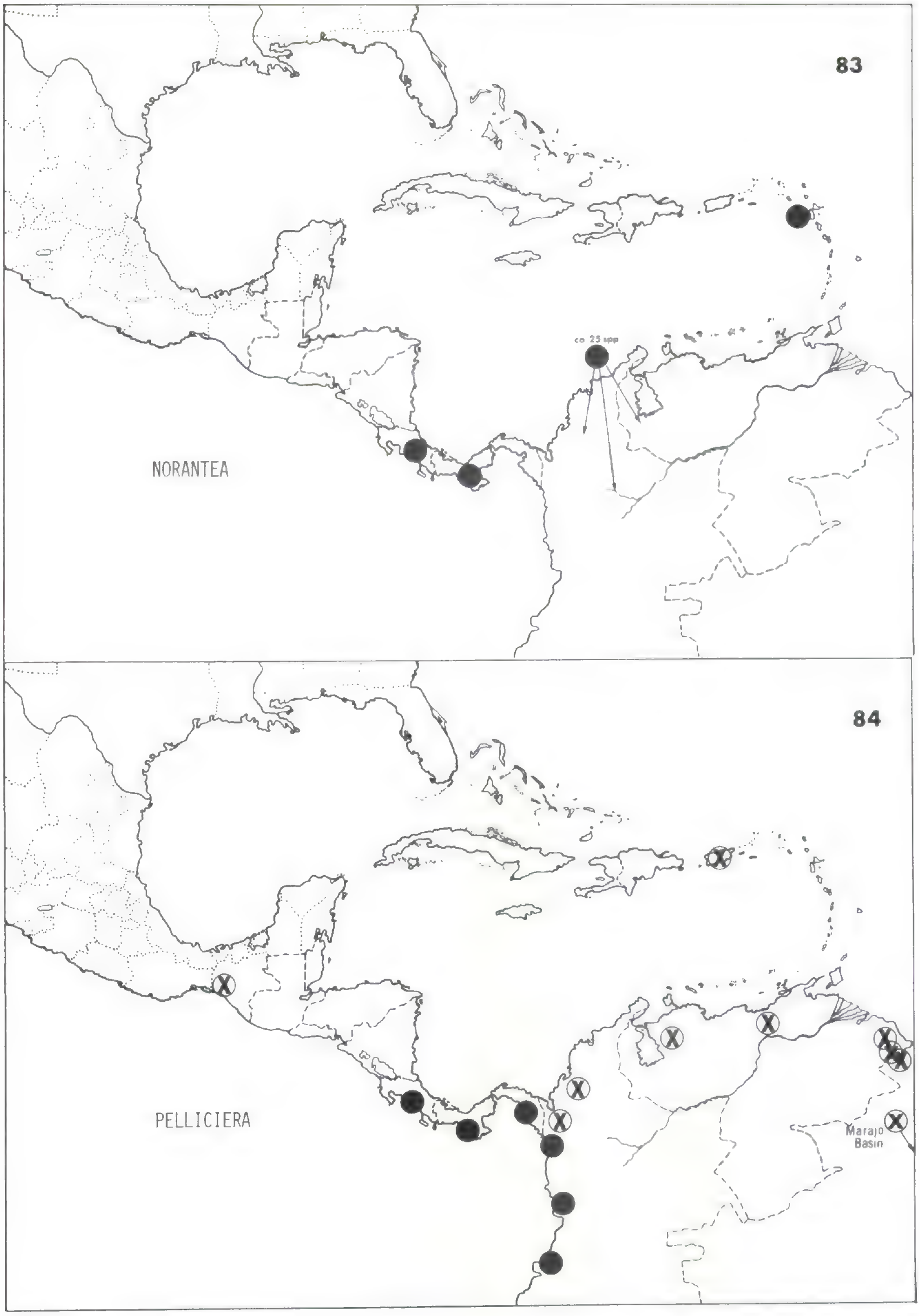
FIGURES 77–78.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—77. *Eugenia*.—78. *Faramea*.



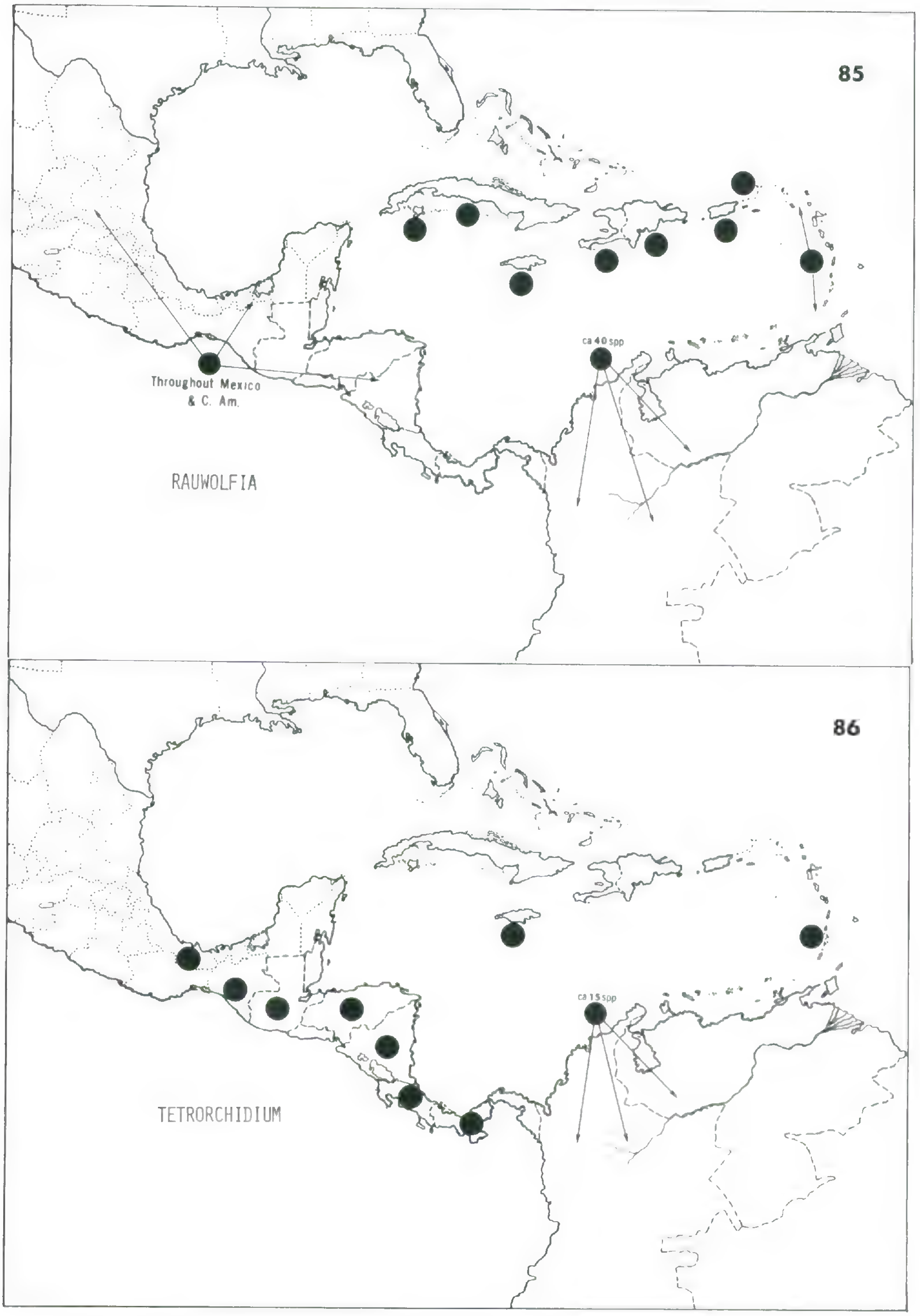
FIGURES 79–80.—Present Latin America distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—79. *Guarea*.—80. *Jacaranda*.



FIGURES 81–82.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—81. *Marcgravia*.—82. *Merremia*.



FIGURES 83–84.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—83. *Norantea*.—84. *Pelliciera*.



FIGURES 85–86.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—85. *Rauwolfia*.—86. *Tetrorchidium*.

Tecoma (Fig. 58)

Tecoma (Bignoniaceae) ranges from Florida to Mexico, Argentina, and the West Indies. There are about 16 species and one, *T. stans,* is native to Puerto Rico. This species is a small evergreen tree (ca. 8 m tall) and has an extensive geographic range. Pollen of *Tecoma* is rare, occurring only at Locality C (0.5%). There are no other fossil records.

Tetrorchidium (Fig. 56–57)

The genus *Tetrorchidium* (Euphorbiaceae) consists of 16 species distributed in Central and South America, the West Indies (but not Puerto Rico), and tropical west Africa (Fig. 86). Gomez-Pompa has recently found the genus in the San Andres Tuxtla area of Veracruz, Mexico (Webster, personal communication, 1969). The plants commonly grow at the upper limits of the montane rain forest. Microfossils are present at all localities and are most frequent at Locality C (1–3%). There are no other fossil records.

Tournefortia (Fig. 59)

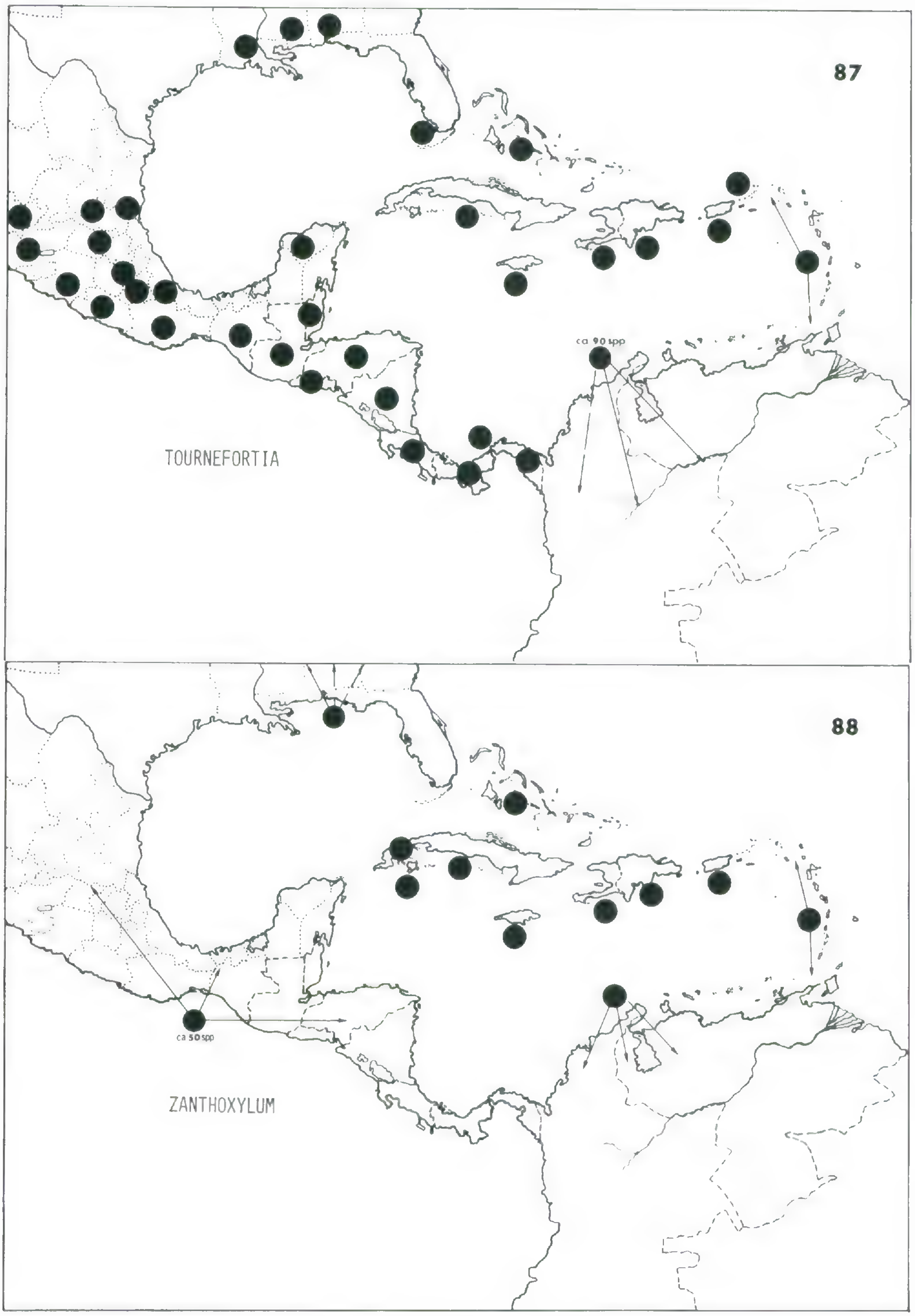
This genus of Boraginaceae is a tropical to subtropical assemblage of about 150 species. At least 130 are known from the New World, and a number occur on the islands of the West Indies (Fig. 87). These small trees and shrubs are common along moist coastal regions where they are often an important feature of primary succession (Richards, 1966). Microfossils were present only in sample A-12 and were rare. There are no other fossil records.

Zanthoxylum (Fig. 47–48)

The genus *Zanthoxylum* (Rutaceae) is a widely distributed assemblage of 20–30 species in temperate and subtropical regions (Fig. 88). At least seven species grow in Puerto Rico — *Z. flarrum, Z. caribaeum, Z. martinicense,* and *Z. monophyllum* being common. These medium-size deciduous trees (7–17 m tall) were common on Puerto Rico and adjacent islands, but because of their highly valued timber they are now scarce and restricted to protected forests (Little & Wadsworth, 1964). In its original habitat *Zanthoxylum* was widely distributed in the coastal limestone and lower montane forests, chiefly of western Puerto Rico. Gleason and Cook (1926) also reported the trees as common in mesophytic coastal forests.

Pollen of *Zanthoxylum* is present at Localities B and C with an abundance of 0.5–1.5%. Berry (1923, 1925, 1939) described *Fagara wadii* from the Miocene of Oaxaca, Mexico, and *F. miocenica* from Trinidad and Cuba. "The occurrence of species apparently transitional in the character of the perianth between *Zanthoxylum* and *Fagara* is ample reason to regard both as components of a single genus" (Brizicky, 1962*b*: 7). The genus *Fagara* is also listed as a synonym of *Zanthoxylum* in LaMotte's (1952) catalogue.

Other Microfossils: In addition to these genera, 120 other types were recovered. Many are referable to family, while others can only be placed in an artificial morphological category. Some of the forms represented are numerous fern



FIGURES 87–88.—Present Latin American distribution of genera identified from the San Sebastian (Oligocene) Formation, Puerto Rico.—87. *Tournefortia*.—88. *Zanthoxylum*.

spores similar to many genera of Polypodiaceae, about 15 types of palm pollen, and representatives of Bombacaceae, Burseraceae, Caryophyllaceae, Ericaceae, Euphorbiaceae, Gramineae, Magnoliaceae, Malpighiaceae, Nyctaginaceae, Oleaceae, Polygonaceae, Proteaceae, Rubiaceae, Theaceae, and Tiliaceae. Fungal spores were also common, but in the absence of adequate reference collections, and with little ecological data available for tropical fungi, identification and environmental interpretations were not possible (Graham, 1962*a*).

Discussion

Initial studies of vegetational history in neotropical regions are likely to yield a miscellaneous assemblage of data difficult to integrate into a documented summary of paleoenvironments. Stratigraphic control and environmental trends established through studies of sequential fossil floras provide the necessary context for interpreting paleontological data, and this context is not available for northern Latin America. The San Sebastian assemblage is the only fossil flora known from the Antilles, and it is the only Middle Oligocene flora from Latin America for which recent published information is available. Until other studies are completed only qualified interpretations may be made of geologic events and vegetational response.

New Fossil Records.—One category of data from the Puerto Rican studies is reports of genera with no previous known fossil record. These include *Aetanthus* (Loranthaceae), *Bernoullia* (Bombacaceae), *Brunellia* (Brunelliaceae), *Corynostylis* (Violaceae), *Dendropanax* (Araliaceae), *Faramea* (Rubiaceae), *Hauya* (Onagraceae), *Jacaranda* and *Tecoma* (Bignoniaceae), *Marcgravia* and *Norantea* (Marcgraviaceae), *Pleodendron* (Canellaceae), *Rauwolfia* (Apocynaceae), *Tetrorchidium* (Euphorbiaceae), and *Tournefortia* (Boraginaceae). These 15 genera constitute 35% of the identified microflora.

Oligocene Communities of Puerto Rico.—Thirteen genera (ca. 30%) of the San Sebastian microflora no longer grow in Puerto Rico and represent extinctions after Middle Oligocene times. Three of these (*Norantea, Tetrorchidium, Bombax*) presently grow in the West Indies but not on Puerto Rico; two (*Aetanthus, Catostemma*) are South American; two are Mexican and Central American (*Hauya, Engelhardia*[4]); and three occur in temperate regions of the eastern United States and eastern Mexico (*Fagus, Liquidambar, Nyssa*). The remaining three genera (*Bernoullia, Corynostylis, Pelliciera*) are widespread in Latin America except the Antilles. Changes in the composition of geofloras through time is common, particularly when ecologically comparable taxa are involved. With the exception of the cool-temperate element, these differences in composition between the San Sebastian microflora and the present vegetation of the West Indies do not imply significant climatic changes.

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[4] A single collection is known from Colombia (D. E. Stone, personal communication, 1969).

The arrangement of the Oligocene genera into communities is tentative because of meager ecological data on the modern forms. An estimate of the associations and their composition is presented in Table 3. At least three communities were present: 1) a lowland, coastal brackish-water community of *Rhizophora* and *Pelliciera*; 2) an upland warm-temperate to subtropical community, with several members common along river banks and lake margins and others which are still part of the present elfin or mossy forest of Puerto Rico; and 3) a highland temperate to cool-temperate community of *Fagus, Liquidambar,* and *Nyssa.* Several genera were probably common to more than one association (*e.g., Ilex, Tecoma, Jacaranda, Bursera,* and *Bernoullia*).

Since approximately 75% of the genera identified presently grow on Puerto Rico or in the West Indies, the aspect and composition of the Oligocene communities were similar to those of the present. There were, however, three principal differences. There was the group of seven genera that no longer grow in the West Indies, but which are found in ecologically similar habitats elsewhere in Latin America (*Aetanthus, Catostemma, Hauya, Engelhardia, Bernoullia, Corynostylis, Pelliciera*). A second difference was that of the above group, *Engelhardia* was particularly common. At Locality C pollen of this genus constitutes 31–54% of the microflora (Table 1), indicating it was an abundant and conspicuous element

TABLE 3. Suggested Oligocene communities of Puerto Rico. Asterisk (*) designates plants presently growing in the elfin forest of Pico del Oeste, elevation 1050 m (cited by Howard, 1968).

1. Coastal brackish-water community.

Rhizophora — *Pelliciera*

2. Upland warm-temperate to subtropical community.

**Cyathea*	*Casearia*	*Jacaranda*
Hemetelia (=*Cnemidaria*)	*Catostemma*	**Marcgravia*
Jamesonia (or *Eriosorus*)	*Chrysophyllum*	*Merremia*
**Lycopodium*	*Corynostylis*	*Norantea*
**Selaginella*	*Dendropanax*	*Pleodendron*
Podocarpus	*Engelhardia*	*Tecoma*
Alchornea	**Eugenia*	*Tetrorchidium*
**Bernoullia*	*Faramea*	*Tournefortia*
Bombax	*Guarea*	*Zanthoxylum*
Brunellia	*Hauya*	
Bursera	**Ilex*	

(species also common along river banks and lake margins)

Alchornea	*Rauwolfia*	*Zanthoxylum*
Casearia	*Salix*	
Corynostylis	*Tournefortia*	

3. Highland temperate to cool-temperate community.

Fagus — *Liquidambar* — *Nyssa*

(genera possibly ranging into the higher altitudes)

**Lycopodium*	**Ilex*
**Selaginella*	*Myrica*

that has been eliminated from the flora since Oligocene times. The other six genera were less common (0.5–2.5%). The third and climatically the most significant difference was the presence of a temperate to cool-temperate element (*Fagus, Liquidambar, Nyssa*). The presence of these plants is important in considerations of paleophysiography and will be discussed in a later section.

The gymnosperm element present today on extreme highlands in the Greater Antilles is absent from the microfossil assemblage. In the Dominican Republic the elfin or mossy forest is replaced at the highest elevations by a forest of *Pinus occidentalis*. In view of the prolific pollen production of pine, it is likely that pollen from such a community would be incorporated into the accumulating sediments. The only gymnosperm pollen recovered was a few grains of *Podocarpus* (Table 1). Hollick (1928) reports only *Zamia* from the megafossil flora of Puerto Rico. These data do not reveal the time of introduction of the high-altitude gymnosperm element in the Antillean flora, but this apparently took place in post-Oligocene times.

In addition to the microfossils, Hollick (1928) reported 56 genera of megafossils from the Collazo Shales (Table 4). Several were tentative identifications, and others need verification. Consequently the present megafossil record is of limited use in environmental reconstructions. Pollen of six megafossil genera was recovered (*Hemitelia, Chrysophyllum, Eugenia, Guarea, Malvocarpon* [*cf. Abutilon*], and *Rhizophora*), and others (*Bactris, Palmacites, Palmocarpon, Cassia, Inga, Sophora*) may be among microfossils presently identified only to family (Palmae, Leguminosae). However, the reliability of the megafossil record cannot be established nor comparisons made between the mega- and microflora until the megafossil flora has been revised; at present only 10% of the megafossil genera was found as microfossils.

TABLE 4. Genera of megafossils from the Collazo Shales, Puerto Rico (Hollick, 1928). Asterisk (*) indicates genus also represented by pollen.

Algae	*Copaiva*	*Musophyllum*
Chondrites	*Cynometra*	*Myrcia*
Ferns and Allies	*Dipholis*	*Myrsine*
**Hemitelia*	*Echites*	*Oreodaphne*
Isoetes	*Echitonium*	*Palmacites*
	**Eugenia*	*Palmocarpon*
Gymnosperms	*Ficus*	*Palmophyllum*
Zamia	**Guarea*	*Pithecellobium*
	Guettarda	*Plumiera*
Angiosperms	*Hancornia*	*Protorhipis*
Acrodiclidium	*Hufelandia*	*Psidium*
Aniba	*Icacorea*	*Ramulus*
Annona	*Inga*	**Rhizophora*
Apocynophyllum	*Iriartea*	*Sapindus*
Aspidosperma	*Juglans*	*Sapota*
Bactris	*Lonchocarpus*	*Sideroxylon*
Cassia	**Malvocarpon*	*Sophora*
**Chrysophyllum*	*Manicaria*	*Stylogyne*
Coccoloba	*Melicocca*	*Trichilia*
Combretum	*Misanteca*	*Zizyphus*

Oligocene Climates and Paleophysiography.—In the preceding section it was noted that about 75% of the identified Oligocene flora presently grows in the West Indies. Of the 13 genera no longer present, 10 grow in habitats similar to those available on Puerto Rico. Consequently the Oligocene climates and general environmental conditions must have been comparable to those of the present. These conditions include an insular environment, although considerably greater in extent than the present landmass of Puerto Rico; a central highland with greater relief than at present; trade winds from the northeast during the winter months, shifting to the east and southeast by July; a rainfall near 180 inches on the windward slopes with a rainshadow effect reducing annual precipitation locally to near the present 10 inches to the lee; and a mean annual temperature of about 78° F on the south coast to several degrees less than the present 70° F in the mountains.

The most significant difference between the Oligocene communities and those of the present was the temperate element in the fossil flora. If Oligocene climates in the Antilles were comparable to those of today, accounting for the distinct similarities between past and present vegetation, physiographic relief must have been greater. The higher altitudes provided the temperate environments required by *Fagus, Liquidambar,* and *Nyssa,* without altering conditions necessary for the growth of more tropical species.

An estimate of physiographic relief in the Greater Antilles during the Oligocene may be made from two kinds of evidence. One is on the basis of the vegetation on present highlands compared to those required by the temperate fossil communities. The highest present elevation on Puerto Rico is Cerro de Punta, 1,338 m, where the vegetation is an elfin or mossy forest (Howard, 1968). In Cuba the highest elevation is Pico Turquino, about 2,000 m. The vegetation there is similar to that on Cerro de Punta. The highest altitude in the Greater Antilles is Pico Duarte, 3,175 m, in the Dominican Republic. The vegetation of Pico Duarte (Holdridge, 1945; G. I. Gastony, personal communication, 1969) is a rocky, windswept, open community of *Pinus occidentalis* with festooning lichens reminiscent of the elfin forest at lower elevations. Other plants at the summit include *Pellaea ternifolia, Plagiogyra semicordata, Lobelia ekmanii, Scrophularia densifolia, Hypericum pycnophyllum, Gnaphalium eggersii, Dendropemon pycnophyllus* (parasitic on pines) and *Lyonia heptamera.* The vegetation on other Antillean highlands has been described by Asprey and Robbins (1953; Jamaica), Howard (1968; Puerto Rico), Seifriz (1943; Cuba) and Urban (1909–1910). Several widespread temperate genera are mentioned: *Apium, Aster, Bidens, Clematis, Clethra, Drosera, Eupatorium, Hypericum, Ilex, Myrica, Oxalis, Potentilla, Ranunculus, Rubus, Smilax, Vaccinium, Viburnum,* and others. Absent from this assemblage of herbs, shrubs, and small trees are the larger arboreal forms found in the fossil deposits.

If it is assumed that altitudes greater than at present provided habitats for the growth of a cool-temperate element in an insular environment at 18° N latitude, the mountains of the Greater Antilles during the Lower and Middle Tertiary exceeded 3,175 m (10,300 feet). Erosion and differential subsidence reduced these

heights with concomitant elimination of the cool-temperate habitats. The low percentages (0.5–4.5%) of the arboreal temperate element in the fossil deposits are consistent with the hypothesis that this element grew in a highland habitat removed from the basin of deposition.

In evaluating the possibility of Oligocene highlands that were of significantly greater altitude than those of today, it must be noted that *Fagus, Liquidambar,* and *Nyssa* all presently grow in east-coastal Mexico, most commonly at elevations of about 1,800 m (6,000 feet). This is a continental rather than insular environment, however, which is not as affected by the Guiana-Caribbean-Florida Gulf Stream current. Further, although these floristic data may only suggest the possibility of Oligocene highlands greater than 3,175 m, this estimate of paleophysiographic conditions in the Greater Antilles is supported by recently available geologic data. The following information has been provided by R. P. Briggs, U.S. Geologic Survey, San Juan.

> There is no good evidence for the existence, prior to the middle or late part of the Late Cretaceous, of any sizable islands or landmasses in this part of the crust of the world. From that time probably through the middle Eocene some reasonably good-sized islands may have been present, but nothing approaching the size of Puerto Rico today, rather perhaps more of the order of some of the Virgin Islands.
>
> After the middle Eocene there was great crustal uplift, forming a landmass considerably greater than exists today, something perhaps approaching 100 miles north to south and surely connecting with the Virgin Islands on the east and probably with Hispaniola on the west. It is quite possible that elevations on this landmass approached 15,000 feet.
>
> This estimate is based as follows. An oil test well on the north coast of Puerto Rico revealed the middle Tertiary San Sebastian Formation resting on an eroded volcanic basement at a depth presently about 5,500 feet below sea level. The present highest point on Puerto Rico is 4,390 feet. This gives a present elevation of Cerro de Punta, above the eroded basement, of a little less than 10,000 feet. Our evidence though shows that there probably was differential subsidence, with the coastal area subsiding somewhat more than the present interior area. But, considering later erosion and the fact that the unconformity probably goes to somewhat greater depth northward beneath the Atlantic Ocean, I would not be surprised if there were 10,000 feet of relief at the time of deposition of the Middle Tertiary rocks in the test well. Perhaps there was a considerably greater relief at the maximum time of uplift, probably in the late Eocene.
>
> You estimate the maximum altitude of Puerto Rico during the middle Oligocene to have been between 6,500 and 7,000 feet above the sites sampled. If we average the present elevations of your sites to 1,000 feet and the average highlands of Puerto Rico to about 4,000 feet, it would appear you are thinking in terms of 3,500 to 4,000 feet of post-middle Oligocene erosion. Going back to my oil test well *versus* present relief estimate, this certainly would seem to make your estimate and my estimate similar. That is 1,000 feet plus 6,500 feet plus 5,500 feet equals a minimum altitude of 13,000 feet.
>
> Of course, much of what I said above is grossly oversimplified, and there is evidence for differential subsidence. Despite this, I think it is safe to say that the relief of ancestral Puerto Rico from Late Eocene to Middle Oligocene time was appreciably greater than exists today. It is also fair to say it was being degraded at a very fast rate.

A comparison of Table 1, Localities A and B with Fig. 4 reveals other details of the vegetation, physiography, and some facies control of the microfossils. At Locality A (second column, Table 1) all identified genera are represented at 2.5% or less except *Rhizophora* which constitutes up to 96% of the microflora. This site marks the approximate position of the shoreline during the Middle

Oligocene bordered by a mangrove swamp of *Rhizophora mangle* and *Pelliciera rhizophorae* (the highest percentages of the latter were also found at Locality A).

Samples 19, 25, and 40 from Locality B (Fig. 4) are coalified lignites, and *Rhizophora* pollen makes up 61–77% of the samples. Samples 15 and 33 are clays (high mineral content), *Rhizophora* pollen constitutes 1% of sample 15 and was absent from sample 33. The alternate layering of organic-rich *versus* mineral strata indicates the shoreline was vacillating, probably in response to gradual short-term pyrogenic (rather than eustatic) changes. During the times of subsidence mangrove vegetation dominated at Locality B and the developing soils incorporated a large amount of organic material. With slight and gradual short-term emergence the site was drained, *Rhizophora* was eliminated at its inland boundary, and more upland vegetation became established on soils of greater mineral content. One of the plants commonly approaching sites vacated by the mangroves was *Engelhardia*. At each locality it increased considerably more than other species as *Rhizophora* decreased (*e.g.*, from a maximum of 3% where *Rhizophora* is abundant to 54% where it is scarce). The reciprocal relationship in percentages of *Rhizophora-Pelliciera* and *Engelhardia* pollen reflects the structural instability of the Oligocene shoreline and records the response of these communities to the orogenic changes characterizing the Caribbean Basin during Middle Tertiary times.

Pathways of Migration.—Equatorial climatic belts are known to have extended considerably beyond their present limits during the Early and Middle Tertiary. The Eocene Goshen flora of western Oregon, near latitude 44 degrees north contains a significant tropical element (Chaney & Sanborn, 1933), and even the revised Tertiary floras of Alaska are yielding some species of tropical affinities (Wolfe, personal communication, 1969). Geological evidence from the Antilles reveals the presence of larger and more continuous landmasses (lessening the physical, oceanic barrier to migration), and paleobotanical data reveal climatic conditions favorable to the interchange of northern and southern elements. That many southern species actually did extend into the southeastern United States is evident both from paleobotanical studies of Mississippi Embayment floras and floristic affinities of the modern communities (Graham, 1965*b*). The question is whether the Antillean Arc or the Isthmian-coastal Mexico region was the principal migration route between the North and South American biotas during Early Tertiary times. Data from Puerto Rico make possible some preliminary speculations, although results from our studies in Panama and Veracruz, Mexico, may require revision of these.

If ancestral Puerto Rico was a landmass some 100 miles wide and included at least the Virgin Islands, Puerto Rico, and Hispaniola, the sea barrier between the West Indies and the southeastern United States may seem significantly reduced. However, the Tertiary seas extended northward across at least part of peninsula Florida, and Oligocene strata are exposed in southern South Carolina, Georgia, Alabama, Mississippi, and as far as 120 miles inland along the Texas coast (Fig. 89). In eastern Mexico and the Yucatan Peninsula, the closest point between Mexico and the Antilles (Cuba), the inland extent of Oligocene seas was

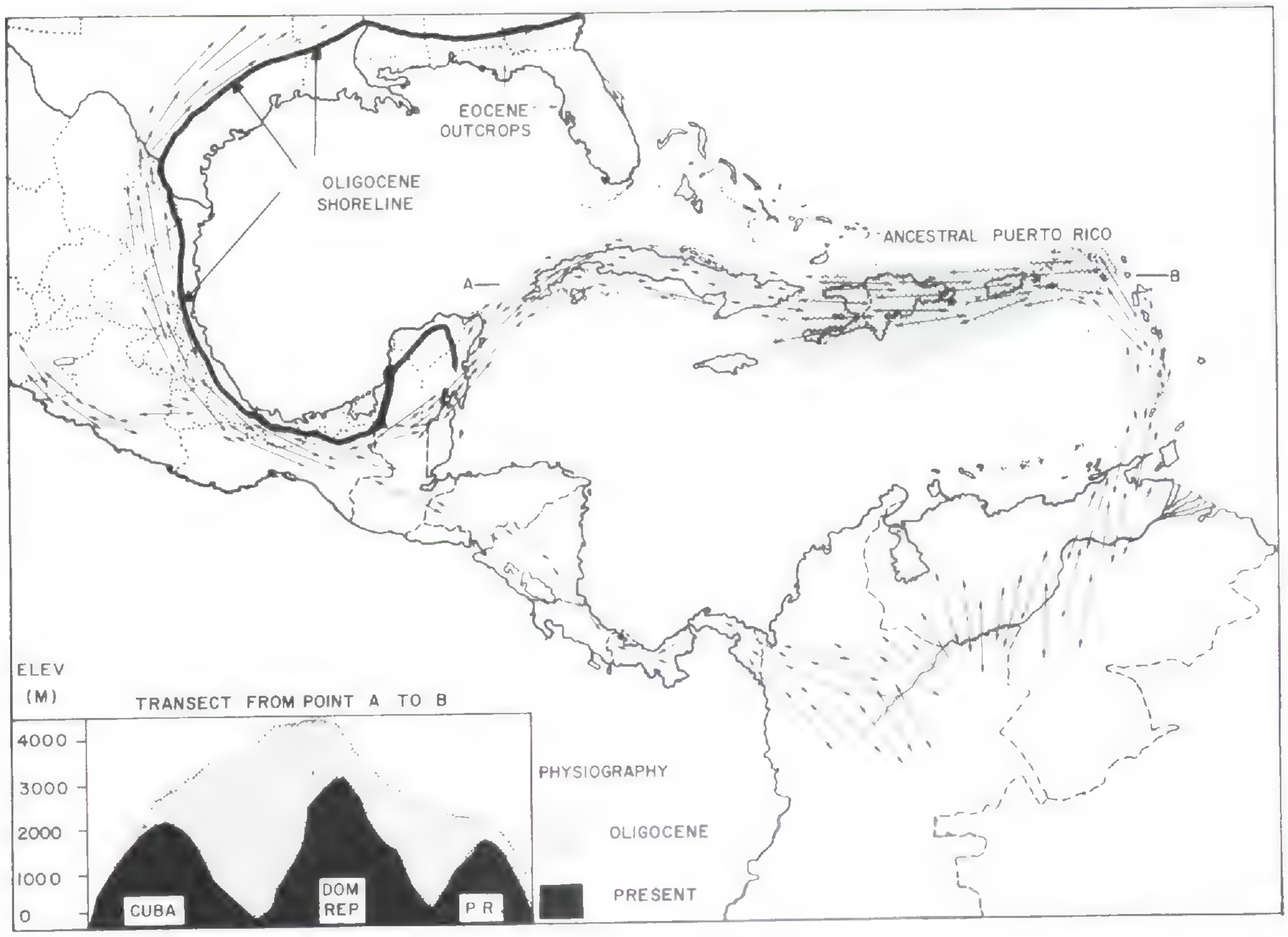

FIGURE 89.—Paleophysiography and Caribbean migration routes during the Middle Oligocene.

considerably less (Salas, 1968). The maximum dimensions of ancestral Puerto Rico, its east-west connections (*viz.*, with Cuba, Yucatan, and the Lesser Antilles), and the history of other islands in the Caribbean are not well known, but available evidence suggests the physical barrier between the southeastern United States and the Greater Antilles during the Middle Oligocene was probably more extensive than at present; between the Greater Antilles and Mexico it probably was no greater than at present and possibly less.

A second approach to evaluating the Antilles as a Tertiary landbridge is by analysis of the floristic affinities of the Oligocene vegetation. Fourteen genera of the Puerto Rican Oligocene flora no longer grow in the West Indies. All 14 are Mexican (commonly eastern Mexican), Central and northern South American. Those genera which may appear to reflect affinities with the eastern United States (*Fagus, Liquidambar, Nyssa*) also grow in Latin America (*e.g.*, eastern Mexico). The same would hold if Hollick's (1928) identification of *Juglans* were included. Thus the 44 identified genera of the San Sebastian Oligocene flora all have affinities with northern Latin America, and none have exclusive affinities with the southeastern United States.

On the basis of these geological and botanical considerations a preliminary model may be made of Tertiary migrations along the Caribbean Basin (Fig. 89). The time of maximum extent of tropical climates (Early Tertiary) corresponds with the period of extensive uplift and maximum availability of land surface in

the Antilles. In the absence of both physical and climatic barriers, two migration routes were available for extension of tropical and subtropical species into northern regions—the Isthmian-coastal Mexico route and the Antillean Arc. Those species migrating along the former were able to extend into southern United States (*cf.* genera listed by Ball, 1931, 1939; and Berry, 1916 from Eocene deposits). After Middle Oligocene times these tropical elements either became extinct as a result of climatic trends toward cool-temperate conditions, evolved new ecotypes capable of growing under temperate environments (*e.g., Dirca,* Thymelaeaceae; *Asimina,* Annonaceae; *Diospyros,* Ebenaceae) or survived in subtropical outliers such as the southward expanding Florida peninsula (*e.g., Rhizophora, Laguncularia, Tillandsia, Avicennia, Annona, Dipholis;* Graham, 1965*b*).

The interchange of species along the Antillean Arc between South America and east coastal Mexico (Yucatan) was facilitated by greater landmasses and physiographic diversity which provided an array of habitats. Further northward migration was hindered, however, by an oceanic barrier at least as extensive as at present. Regarding the Bahama Islands which presently form the nearest complete connection between the Greater Antilles and southeastern United States, Butterlin (1956: 173) states that from the Lower Cretaceous "until the Quaternary, shallow calcareous sedimentation consisting of reef or inter-reef formations were established in the marine subsidence basin. The area remained out of the scope of the orogenic forces and these series are not folded. During the Quaternary and particularly the Pleistocene, relative movements of the marine level and submerged shelf have enabled the latter to emerge."

Reconstruction of the geologic history of the Florida peninsula is complicated by Pliocene and younger strata overlying the Lower and Middle Tertiary deposits. Much of the pertinent data must come from studies of subsurface geology based on available well cores. According to the correlation charts of Cooke, Gardner, and Woodring (1943) the Ocala, Byram, and Suwannee Limestones are marine units deposited during Upper Eocene through Middle Oligocene times. Further, the Suwannee Limestone is encountered in subsurface cores as far north as Fort Pierce, and isopach maps (Toulmin, 1955) show that it thickens to the south. These data mean that at least the lower one-third of the Florida peninsula was submerged during much of Eocene and Oligocene times.

In the vicinity of Ocala, Florida, and in the northern Florida-Georgia region exposed Eocene strata are surrounded by younger rocks. Geologically this could mean these areas were emergent during Middle and Late Tertiary times and no younger overlying rocks were deposited. According to this interpretation these areas would be islands, and their presence would reduce the oceanic barrier between the Antilles and the southeastern United States. Another possibility is that the Eocene units were not emergent during post-Eocene times but have been exposed through erosion of the overlying beds. The Eocene rocks in question form the cap of the Ocala Uplift. The association of the beds with a geomorphic feature of positive relief favors the latter interpretation. According to Stringfield (personal communication, 1969) the outcropping of the Ocala Limestone is an erosion feature and not due to continuous post-Eocene emergence. In summary, the gelogical

evidence indicates that much of peninsula Florida was submerged and no intervening islands were present during the time the floristic composition of the San Sebastian flora was developing.

In contrast, the Lesser Antilles, forming the present connection between the Greater Antilles and northern South America, were probably significant landmasses during much of the Tertiary. According to Butterlin (1956) "the Dutch islands must have remained above water (from Cretaceous) until the Upper Eocene. During that last period the sea flooded the region depositing limestones and marls. . . . The islands reemerged again and the sea did not flood the area until the Miocene."

As a consequence of the difference in physiographic history between the northern and southern connections of ancestral Puerto Rico, the Oligocene communities include numerous elements common to the present plant associations of eastern Mexico, Central and northern South America, and are floristically distinct from the vegetation of the southeastern United States. The herbaceous and shrubby temperate elements in the modern Antillean flora, including many species with broad ecological tolerances, constitute either holdovers from older Tertiary times (the distinctly cool-temperate arboreal forms being eliminated through erosion of the highland habitats) or modern introductions through natural, long-distant dispersal and anthropogenic factors.

Summary

In the preceding section a model has been presented for early Tertiary migration patterns around the Caribbean Basin (Fig. 89). The model is consistent with paleobotanical and geological data as presently understood, but it can also be evaluated on the basis of natural (*i.e.*, non-anthropogenic) distribution patterns of modern organisms. We accept as a generalization that animal, particularly land vertebrate, distribution is influenced to a considerable extent by the range of the plants serving as a source of food and protection. If this is true, and if the model is essentially correct, certain plants and animals should have at least vestiges of a distribution pattern consistent with Fig. 89. The organisms exhibiting this pattern should be 1) those whose origins date back at least to Early or Middle Tertiary times, and 2) those with conservative distribution potentials and without exceptionally broad ecological tolerances (*e.g.*, non-weedy species). Changes in the range of such organisms can be expected to commonly reflect changes in the physical and/or climatic barriers to migration.

Based on the model, plant and animal species of the southeastern United States having affinities with Latin America should show strongest affinities with eastern Mexico and/or Central America and/or northern South America, rather than with the flora and fauna of the Antilles even though the latter is geographically closer. Although the literature of biogeography can be surveyed for examples pertinent to evaluating the model, critical tests can only be made by specialists in various groups who can differentiate between biologically meaningful patterns and those created by poor taxonomy. One range reflecting the expected pattern is that of the plant genus *Cuphea* (S. Graham, personal communication, 1969). The spe-

cies occurring in the southeastern United States are generally more closely related to those of Mexico, Central and even northern South America than to those presently growing in the Antilles. Similarly several genera of trees in the eastern deciduous forest of the United States occur disjunct in eastern Mexico and regions to the south and are absent in the Antilles. Martin and Harrell (1957) cite similar patterns among the vertebrates.

A final consideration relates to the history of the isthmian region during lower Tertiary times. Studies on the vegetational history of Panama are just beginning, but according to Woodring (personal communication, 1969) study of the geology and fossil faunas reveals that the area was submerged during at least the major part of the Tertiary (from Paleocene to Early Pleistocene). At present it is not possible to determine the effectiveness of the oceanic barrier to interchange between the terrestrial plant communities to the north and south. It seems reasonable, however, considering the relatively emergent condition of the Antillean Arc and east-coastal Mexico region compared to the Isthmus, that the former may have served as the principal migration route between the North and South American biotas during the Tertiary.

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WOOD ANATOMY OF GOODENIACEAE AND THE PROBLEM OF INSULAR WOODINESS[1]

SHERWIN CARLQUIST[2]

ABSTRACT

Goodeniaceae, a basically herbaceous family with a clear center of origin and diversification in Australia, has become woody to a limited extent in several genera and genuinely arborescent in some species of *Scaevola*. The most woody of these are montane species of Pacific islands. The probable evolutionary patterns of these and correlations between wood anatomy and ecological conditions are reviewed. Quantitative and qualitative data are presented in tabular form for 78 collections of 43 taxa of the family. Xermorphic Goodeniaceae tend to have short, narrow vessel elements with helical sculpturing, whereas the reverse is true in mesic species. Absence of axial parenchyma and abundance of crystals also characterizes xeric species. The predominance of erect ray cells or raylessness, as well as occurrence in a few species of scalariform or elliptical pits on lateral walls of vessels are probably indicators of juvenilism (paedomorphosis). Goodeniaceae do not have libriform fibers, but rather tracheids or fiber-tracheids, with a tendency toward the latter in arborescent species. Multiseriate rays are tall. Correlations between wood anatomy and habit are summarized under the headings: Australian short-lived perennials and short-lived shrubs; montane Pacific species of *Scaevola;* and maritime species of *Scaevola.*

INTRODUCTION

Wood anatomy of Goodeniaceae has been little studied. This no doubt derives from the fact that no species in the family provides any economically used wood. Although a few species of *Scaevola* become small trees, most of the family can be described as herbs. However, a predominantly herbaceous family that becomes woody during its evolution provides interesting patterns of wood anatomy and ought to be an especially valuable subject for that reason. Goodeniaceae is an outstanding example of this mode of evolution.

The center of origin and diversification of the family is obviously Australian. If we take into account *Brunonia* and the recently named *Neogoodenia* (Gardner & George, 1963) and *Coopernookia* (Carolin, 1967), ten of the 16 genera are endemic to Australia. In four genera, only one species extends beyond Australia, and that species occurs in Australia also: *Selliera radicans* (southern and southeastern Australia, Tasmania, New Zealand, Chile); *Velleia spathulata* (eastern Australia, southeastern New Guinea); *Calogyne pilosa* (northern Australia, Moluccas, southern New Guinea, southern China); and *Leschenaultia filiformis* (northern Australia, Moluccas, New Guinea). The remainder of these genera are exclusively Australian species. *Goodenia koningsbergii* occurs only in Indonesia and southeastern Asia, but this is a single species of a large genus. That none of these genera (except *Goodenia*) has preponderantly primitive features for

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ANN. MISSOURI BOT. GARD. 56: 358–390. 1969.

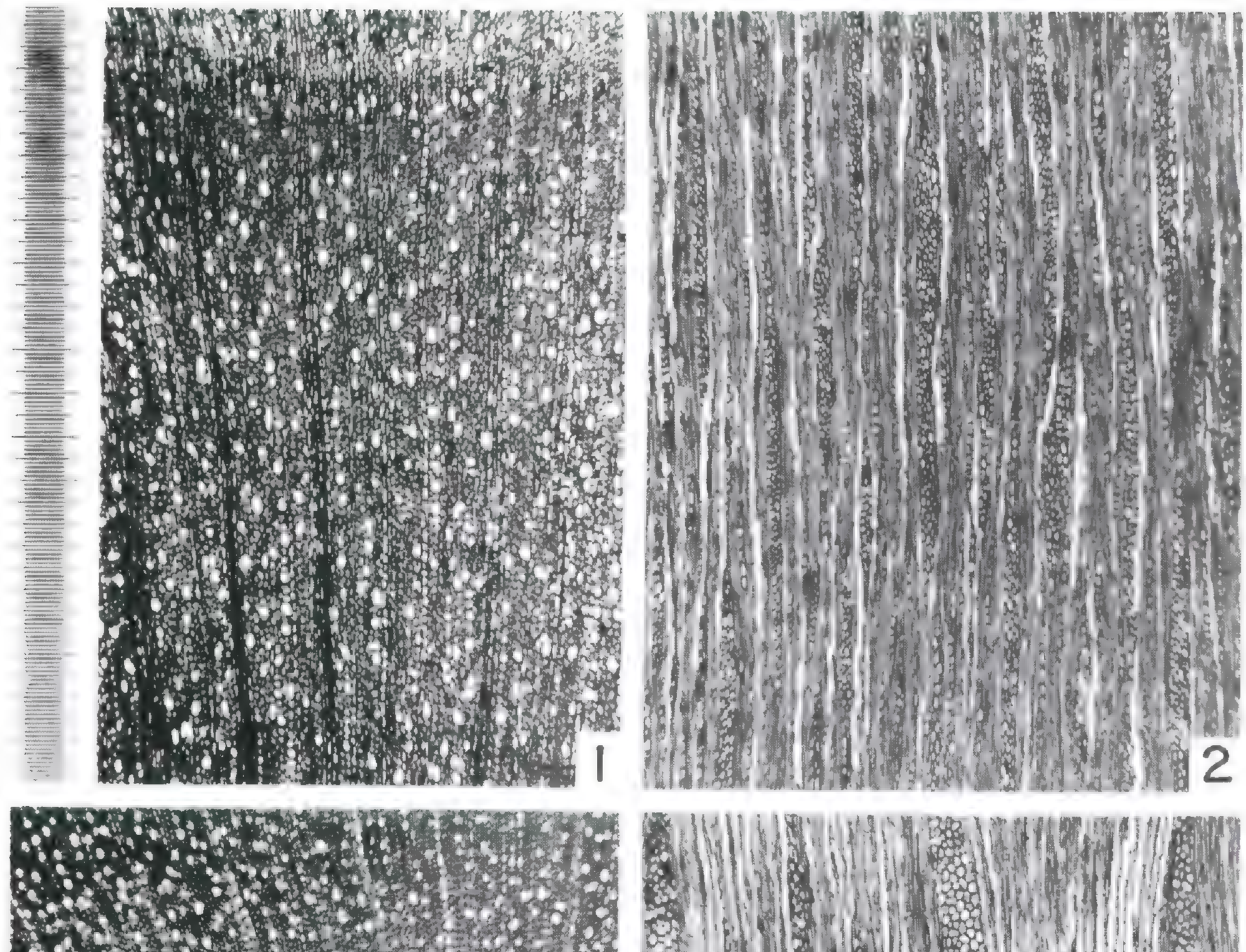
the family suggests strongly that the origin and diversificaion of Goodeniaceae has taken place within Australia. The only other genus with non-Australian species is *Scaevola.* This genus, too, has been regarded as specialized within the family (Krause, 1912; Carolin, 1959, 1966). It is the only genus of the family which becomes markedly shrubby or arborescent. The most arborescent species are *S. gaudichaudiana* and *S. glabra* of the Hawaiian Islands; these can form trees five or six meters tall. On the basis of circumstantial evidence alone, the family has an herbaceous origin and has become woodier on islands. Floral morphology and geographical distribution seem to support this view.

Of the genera other than *Scaevola,* few show any appreciable woodiness. This seems to be related to adaptation to the dry temperate Australian environment. Many Australian Goodeniaceae are annuals or short-lived perennials. The latter are often branched from the base, so that little wood accumulates, and a wood sample, if one can be collected at all, has to be taken from the short rootstock. Wood in this structure is probably not really comparable to wood of a true shrub, and the grain is often so contorted that sections are difficult to prepare and of limited value. Growth forms such as these are related to Mediterranean climates. In the present study, *Dampiera brownii* and *D. glabrescens* represent caudex-bearing perennials, branched from near the base. Short-lived shrubs, usually less than a meter high, are formed by *Goodenia scapigera, G. ovata, Coopernookia polygalacea, C. strophiolata,* and *Verreauxia reinwardtii.* Of these, only *Goodenia ovata* grows in a mesic situation, the eucalypt forests in which tree ferns may also be found. The other shrubby species listed grow in relatively dry sandy areas of Western Australia.

Within the genus *Scaevola* some of the Australian species correspond to the above growth forms, but some are more genuinely woody. *Scaevola sericophylla* and *S. fasciculata* are short-lived shrubs of Western Australian scrub heath, whereas *S. crassifolia, S. nitida,* and *S. porocarya* are larger shrubs (to one meter or more), probably of relatively short duration (10 years or less). These three species occupy sites near the coast: *S. crassifolia* is typically a dune plant. *Scaevola spinescens* is a shrub, usually less than a meter in height, that grows near salt lakes in Western Autralia and other states of Australia. *Scaevola tomentosa,* although a close relative of *S. spinescens,* is a prostrate shrub of coastal limestones in Western Australia.

Scaevola holosericea and *S. paludosa* are Australian species, little more than perennial herbs, in which only a few older stems have sufficient wood for study. None of the Australian scaevolas could be called clearly mesic in habitat except *S. oppositifolia,* a scandent species of disturbed places in wet forests of Queensland. In localities north of Australia, including islands as far north as the Philippines, *S. oppositifolia* has been given a multiplicity of segregate specific names. These have been justifiably designated as synonyms by Leenhouts (1957*a*).

With respect to taxonomy, Krause (1912) has placed all of the Australian species studied here in section *Xerocarpaea* except *S. spinescens, S. tomentosa, S. oppositifolia,* and the wide-ranging *S. taccada. Scaevola spinescens* and *S. tomentosa*



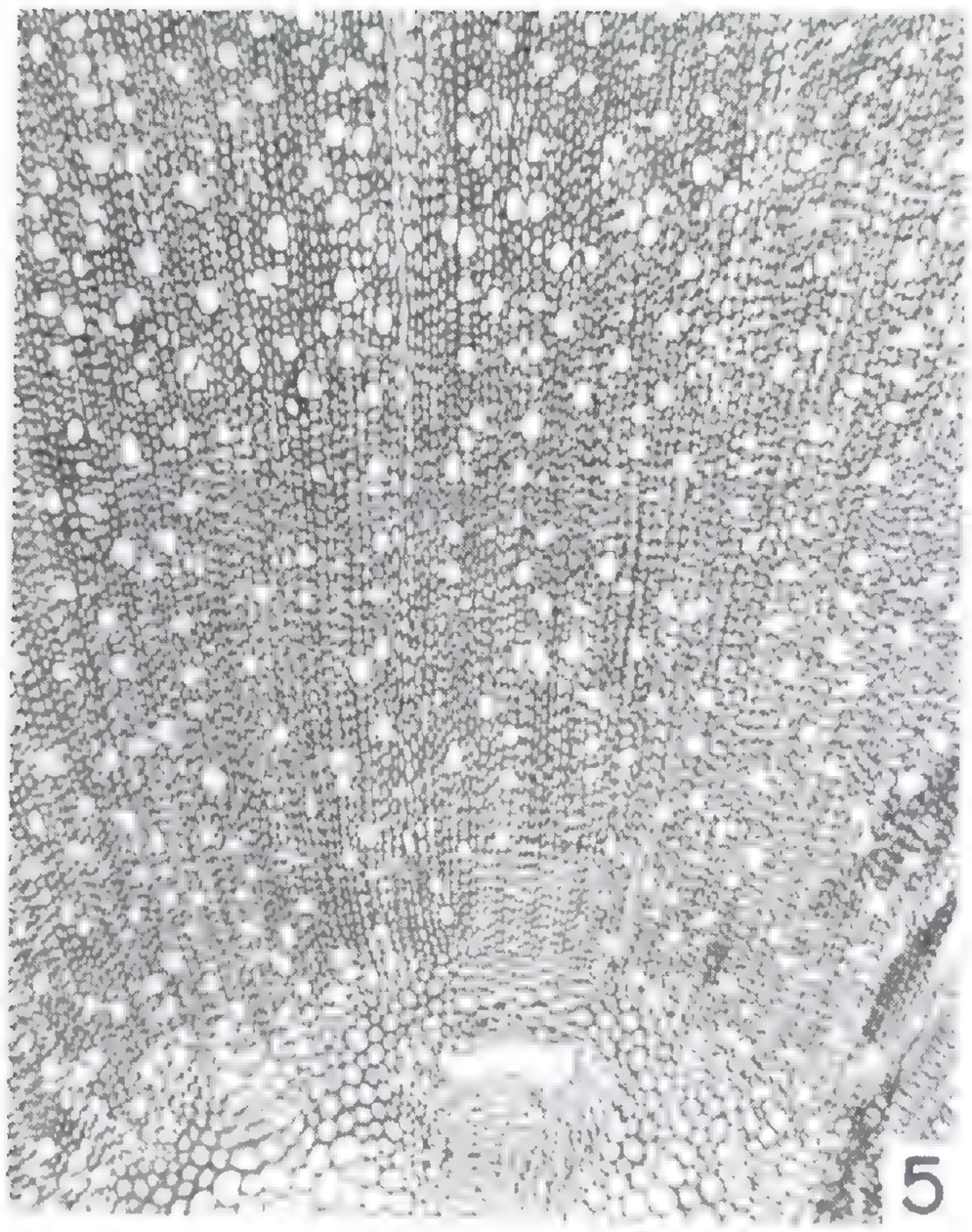
FIGURES 1–4.—Wood sections of *Coopernookia*. — 1–2. *Coopernookia polygalacea* (*Carlquist 3475*).—1. Transection. Note narrowness of vessels.—2. Tangential section. Rays are numerous, narrow. — 3–4. *Coopernookia strophiolata* (*Carlquist 3393*).—3. Transection. Note growth rings.—4. Tangential section. Rays are few, wide; light portions are the wider vessels from early wood. — Scale to the left of Fig. 1 is a stage micrometer photographed at the same scale as Fig. 1–41. Length shown is 1.8 mm; divisions 10μ each.

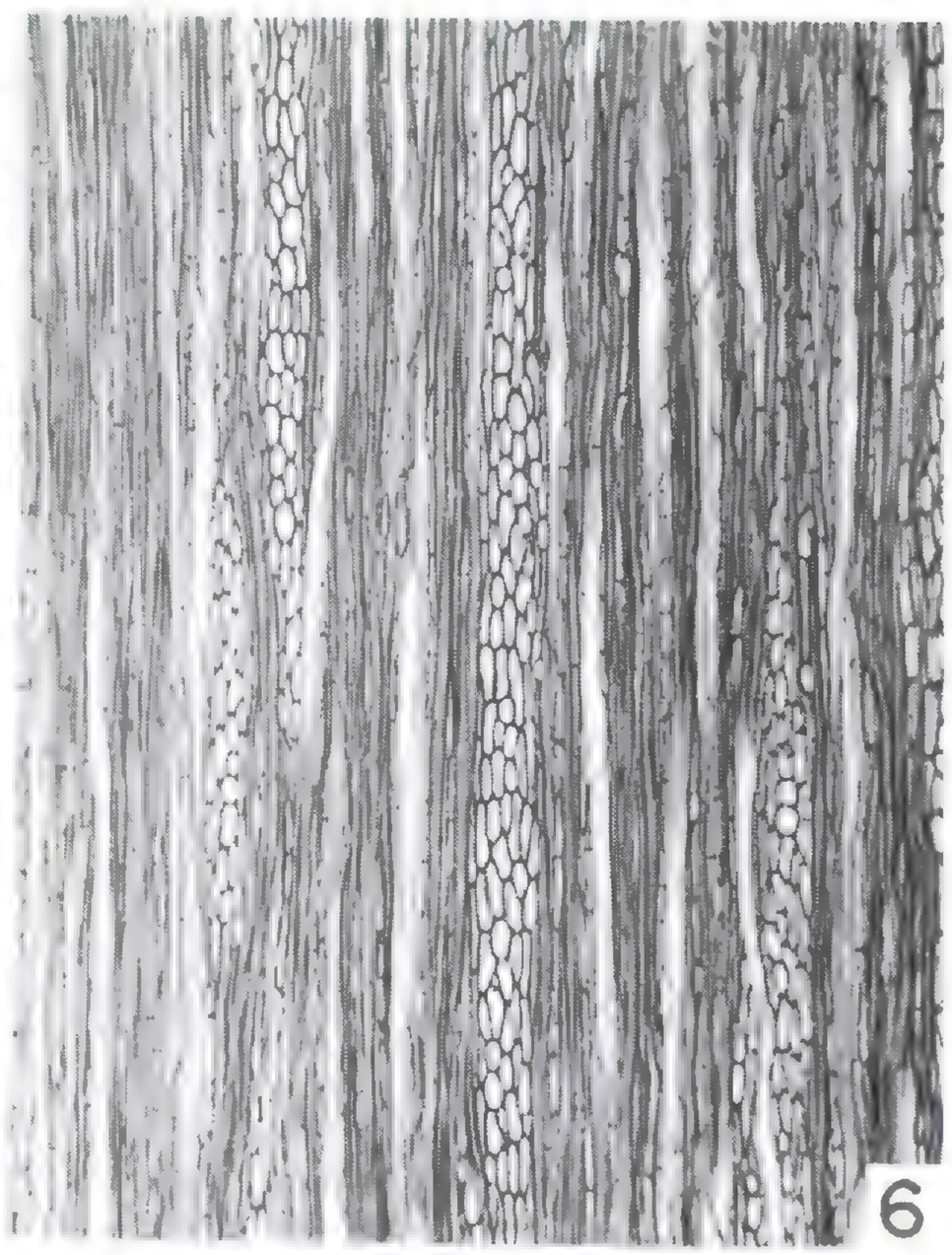
are members of sect. *Crossotoma; S. oppositifolia* belongs to sect. *Enantiophyllum,* and *S. taccada* belongs to sect. *Scaevola.*

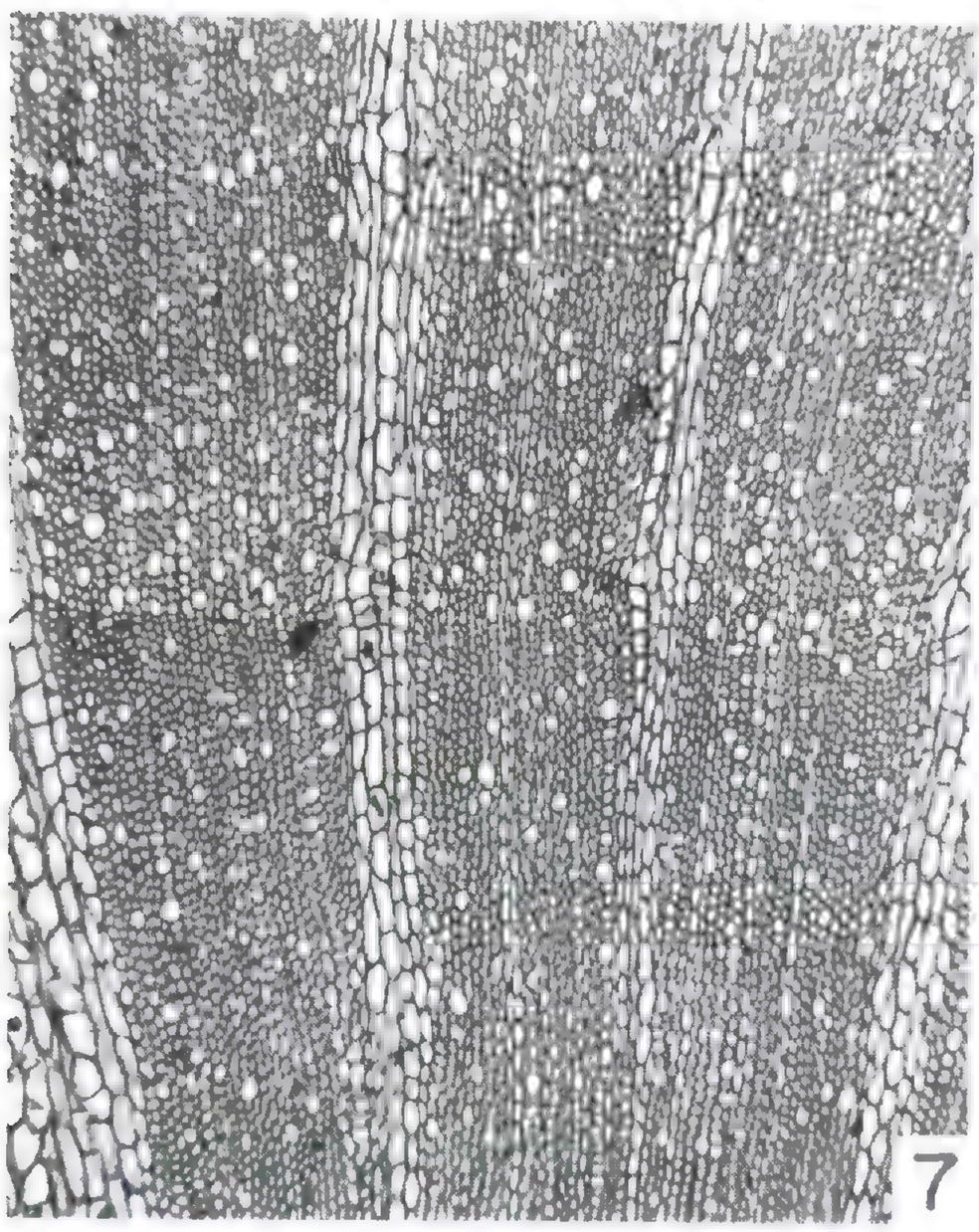
Species of section *Scaevola* (formerly sect. *Sarcocarpaea*), sometimes termed the "fleshy-fruited scaevolas," bear purple or white fruits with a fleshy exocarp attractive to birds and a woody endocarp in which seeds are embedded. Because of the excellence of this dispersal mechanism for long-distance dispersal (Carlquist, 1967), the fleshy-fruited scaevolas have spread around the world. This is undoubtedly a relatively recent, although pre-human, pattern. The widespread pan-Pacific beach *Scaevola, S. taccada,* occurs in Australia and might have originated there. *Scaevola plumieri* does not occur in Australia, but its distribution might be said to represent a radiation from the Australian region. The species of section *Scaevola* are otherwise non-Australian. However, perhaps the closely-related fleshy-fruited sections, *Crossotoma* and *Enantiophyllum* represent remnants of this stock on the Australian continent. *Scaevola calendulacea,* a beach species of eastern Australia, has fleshy white fruits, tinged purple, that float in seawater and remind one of fruits of *S. taccada.* It supposedly belongs to section *Xerocarpaea,* but if so (and that disposition needs to be reinvestigated), it shows rapid evolution of a beach species with fleshy fruits both attractive to birds and dispersible by flotation in seawater. Either interpretation of *S. calendulacea* as a derivative of dry-fruited *Scaevola* species or hypothesizing it as a relict of sect. *Scaevola* stresses the same result—origin of the fleshy-fruited stock termed section *Scaevola* in the Australian region.

Two species of section *Scaevola* are exclusively maritime and distributed by oceanic drift of the fruits: *S. taccada* (also known as *S. sericea, S. frutescens, S. koenigii,* etc.) and *S. plumieri* (also known as *S. lobelia*). Guppy (1917) demonstrated that *S. taccada* fruits can float for a year or more in seawater, while fruits of *S. plumieri* can withstand only four or five months of flotation. *Scaevola taccada* ranges across the Pacific, reaching all tropical Pacific coasts (except the west coasts of Mexico, Central and South America) and coasts of the Indian Ocean, including Madagascar, the Comoro Islands, the Seychelles, the Andamans, and India (Krause, 1912). *Scaevola plumieri* has a more restricted distribution: Florida and the Gulf Coast, the West Indies and south to Brazil; India, Ceylon, east Africa, and south Africa (Stern & Brizicky, 1958; Brizicky, 1966). Its presence on limited areas of the Pacific Coast of North America (Clarion Island; Baja California) is curious and represents an outlier of the above distribution. *Scaevola plumieri* may have a distribution more limited than that of *S. taccada* because of its lesser ability to float in seawater. However, the fleshy purple fruits of *S. plumieri* would lend themselves to transport by birds, especially shore birds (Carlquist, 1967). Chance dispersal by birds may account for the Pacific stations for *S. plumieri.* A new species of *Scaevola* from Socotra (St. John, 1962) may be a derivative of *S. plumieri;* phytogeographically, this seems the most likely possibility.

Fruits of *S. taccada* are distributed by seawater, but also have been observed to have been eaten by shore birds and transported in that fashion (F. R. Fosberg, personal communication). Both *S. plumieri* and *S. taccada* are definitely maritime in their ecology. *Scaevola taccada* extends short distances inland in Fiji (Guppy,





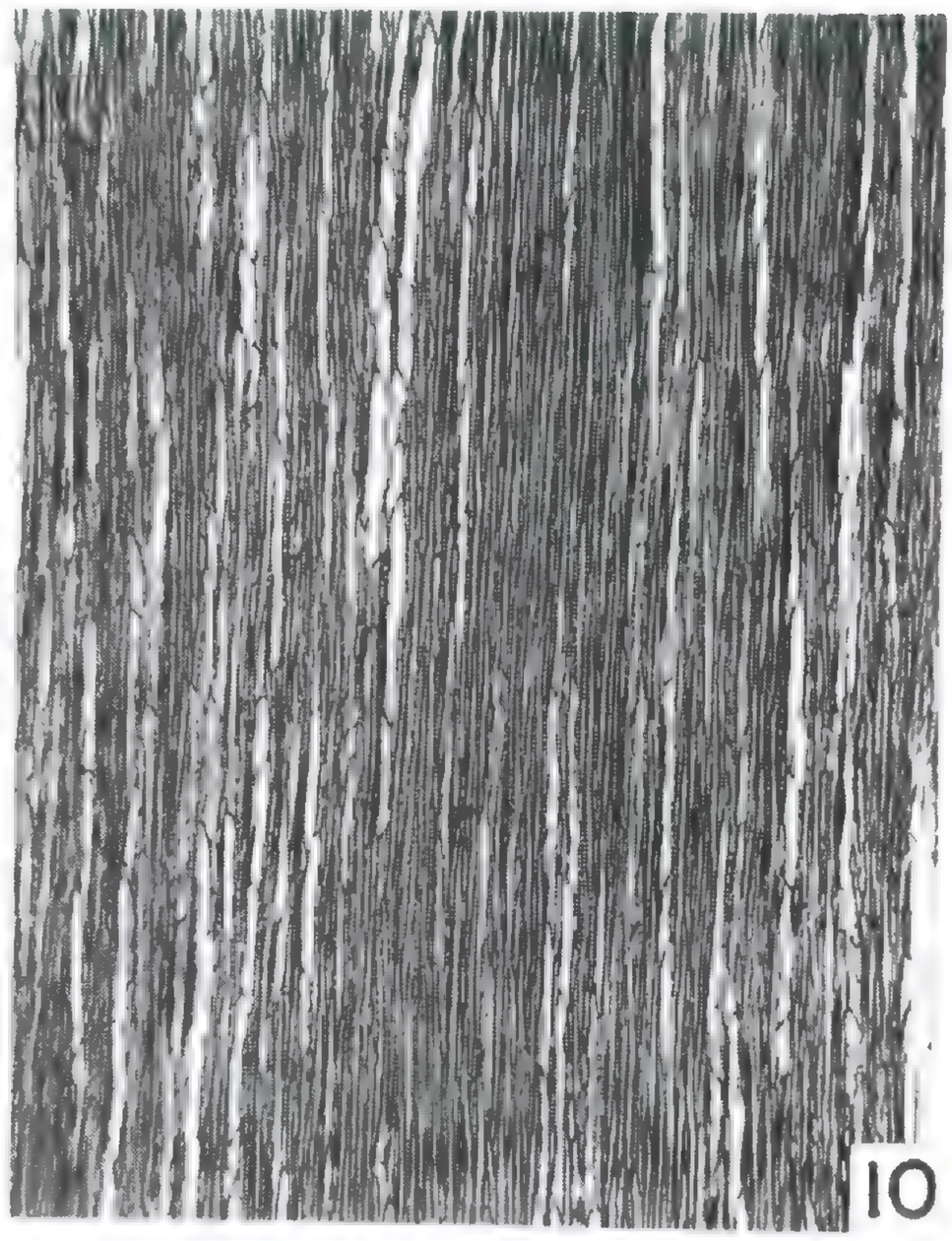


FIGURES 5–8.—Wood sections of *Goodenia* — 5–6. *Goodenia ovata (Carlquist 831).*— 5. Transection. Portion of pith below, showing one of the primary bundles in which secondary xylem does not form; wood is rayless at first.—6. Tangential section from periphery of larger stem. Tall multiseriate rays are visible. — 7–8. *Goodenia decurrens (Carlquist 1308).* —7. Transection.—8. Tangential section. Wide multiseriate rays and many uniseriate rays are evident. — Scale of magnification shown beside Fig. 1.

1906) and Hawaii (St. John, 1952). However, these plants are within the maritime influence and probably are not isolated genetically from beach populations, nor can they become isolated due to the excellent dispersal mechanism of this species. When a littoral insular species cannot become isolated for long periods of time, populations of minor distinction can arise (*e.g.*, *S. taccada* var. *tuamotensis* St. John, 1960), but speciation beyond such minor variants is impossible (Carlquist, 1966*b*). On the basis of these considerations alone, one would not expect *S. taccada* to evolve into montane species. In fact, comparative gross morphology of the fleshy-fruited scaevolas shows that the montane species of Pacific islands form a phyletic series separate from *S. taccada* (or *S. plumieri*). The reverse hypothesis, that the various purple-fruited montane species have each originated independently from *S. taccada* is considerably the more difficult hypothesis and not borne out by the evidence. However, this interpretation was advanced by Brown (1935), who claimed the Marquesan *S. subcapitata* to be a derivative of *S. taccada,* and evidently also by Lauterbach (1908), who regarded the Samoan *S. nubigena* as closest to *S. taccada.* Brown's conclusion is amusing, for though he claims *S. subcapitata* as close to *S. taccada,* he regards a second species, *S. marquesensis,* as close to the Hawaiian *S. procera* (a Kauai population of *S. gaudichaudiana*). However, *S. subcapitata* and *S. marquesensis* seem barely separable, and probably should be united. *Scaevola nubigena* is worthy of specific recognition; it resembles *S. floribunda* of Fiji most closely, and Lauterbach does acknowledge the similarity in leaf shape between these species.

The montane fleshy-fruited scaevolas form an interesting trans-Pacific series. They probably represent a sort of island-hopping, but perhaps not in a perfect sequence (*e.g.*, Samoan derived from Fijian, Fijian from New Caledonia, etc.) from west to east. These insular species, together with *S. plumieri* and *S. taccada,* form a cohesive group. The montane insular species probably originated from a fleshy-fruited ancestor, even if, as Carolin (1966) seems to claim, the dry-fruited habit is primitive for the genus. The interrelationships of species of *Scaevola* is certainly not clear at present, and Carolin's phylogeny of fruit types is open to question. For example, he envisions fruits of *S. mollis* ("Type 3") and *S. chamissoniana* ("Type 2") as independent derivatives from the type represented by an Australian species, *S. porocarya,* and not known outside of *S. porocarya.* However, *S. mollis* and *S. chamissoniana* are very closely related Hawaiian species which very likely derive from a single Hawaiian ancestor, an ancestor that probably resembled the Fijian *S. floribunda* but certainly not *S. porocarya.* The species of sect. *Crossotoma,* with their one-flowered cymes, do resemble the species of sect. *Scaevola* in a number of respects, certainly. A recently-named species of New Guinea, *S. pauciflora* (Leenhouts, 1957*b*), shows similiarity to both sections.

The New Caledonian species of sect. *Scaevola* seem to represent at least two introductions. *Scaevola heckii,* a lowland species of dry serpentine areas, is quite unlike the upland species in habit, inflorescence type, and various other technical features. The upland scaevolas of New Calendonia are, however, closely related to species of islands to the east. *Scaevola montana* in particular is similar to *S. floribunda, S. marquesensis,* etc. Hybrids between *S. montana* and *S. indigofera* may



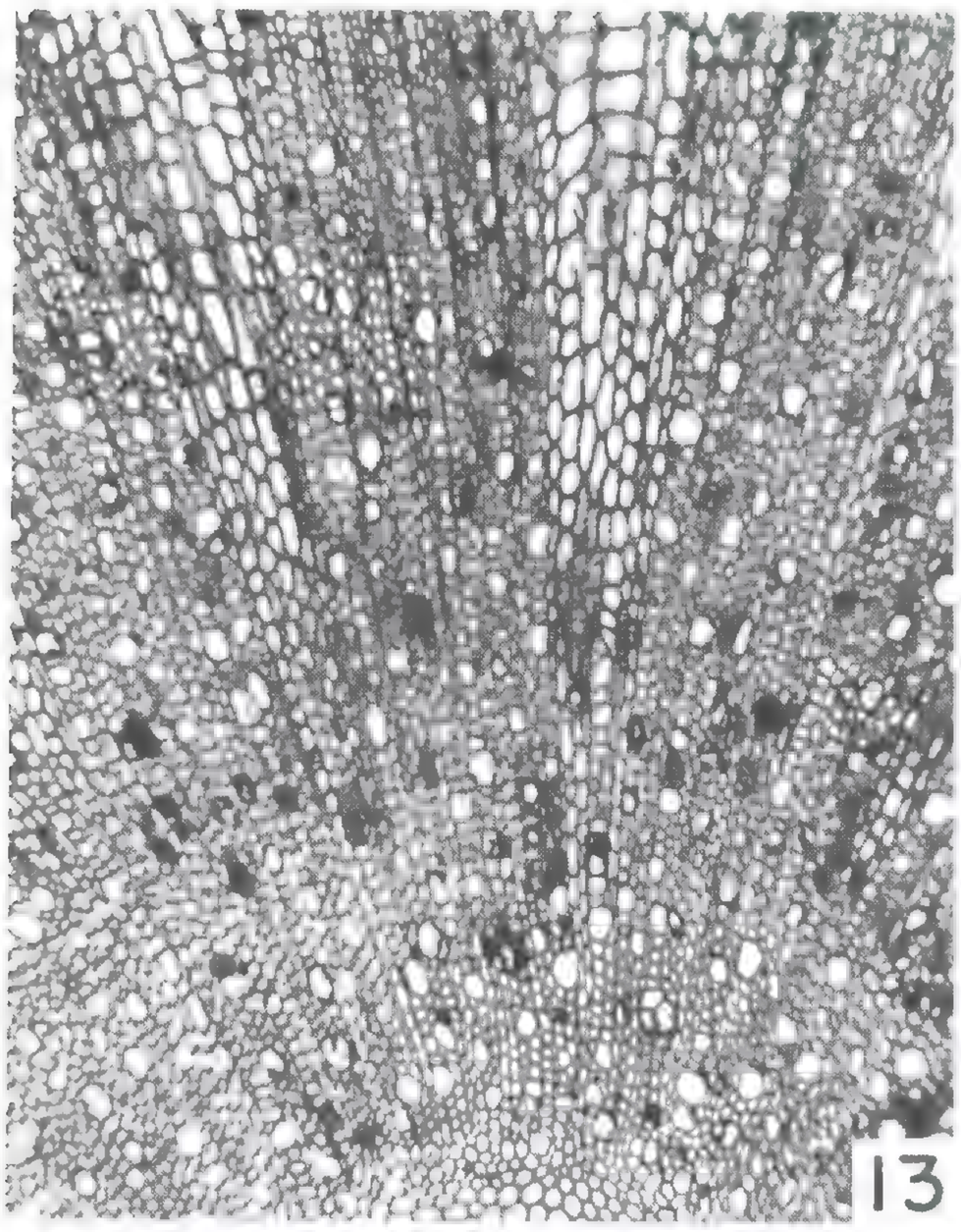
FIGURES 9–12.—Wood sections of *Leschenaultia*. — 9–10. *Leschenaultia splendens (Carlquist 3437)*.—9. Transection, pith below.—10. Tangential section. Note raylessness of wood. — 11–12. *Leschenaultia biloba (Carlquist 911)*.—11. Transection. Lower portion of this photograph is rayless wood.—12. Tangential section, taken from periphery of older stem. Rays have developed at this stage. — Scale of magnification shown beside Fig. 1.

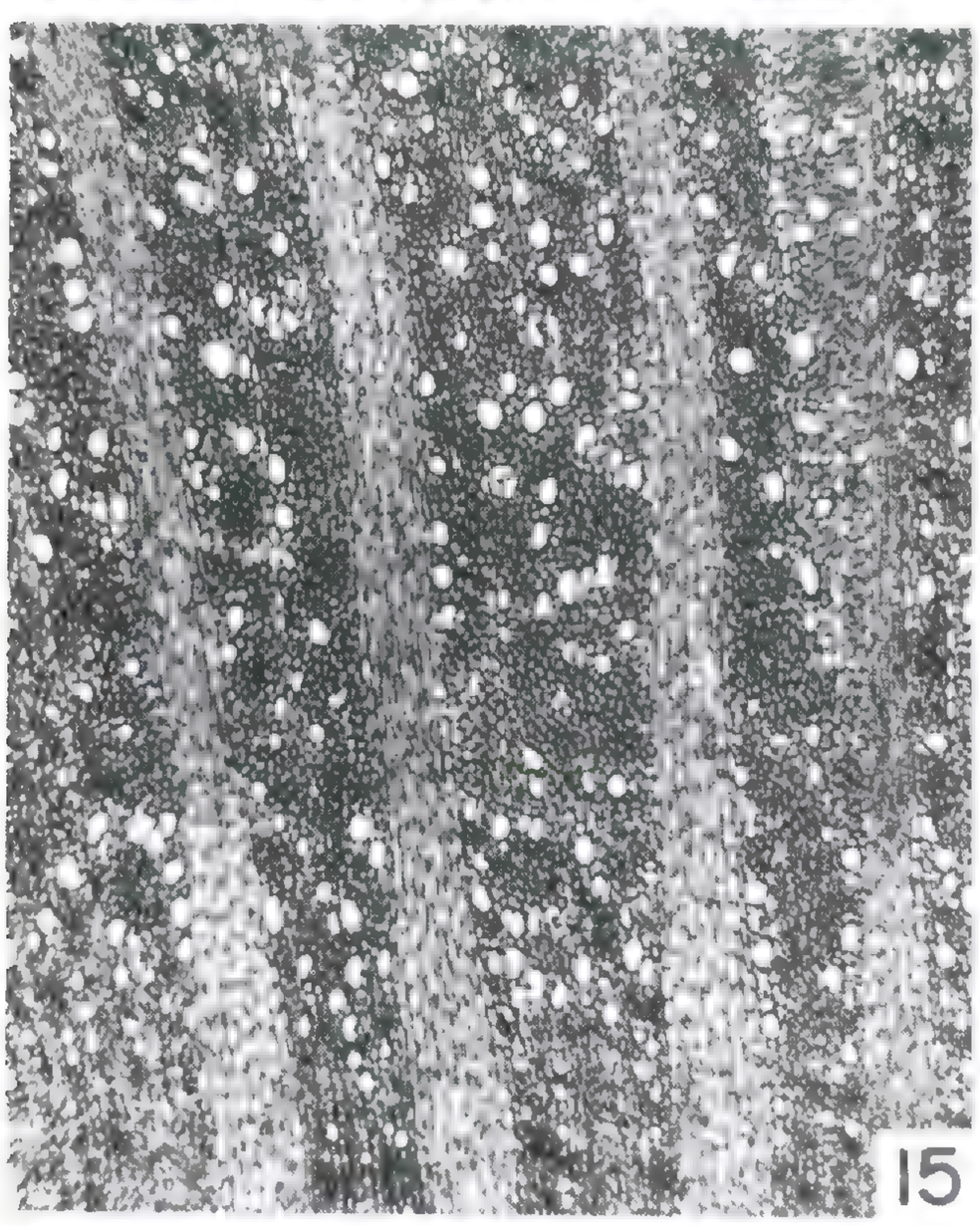
be found in various places on New Caledonia. *Scaevola montana* typically is a lower-elevation montane species, but it comes into contact with *S. indigofera* in some places. Hybrids in New Caledonia scaevolas have very likely been named as species, and study of various taxa in the field in New Caledonia is very much needed. *Scaevola cylindrica* might be such a hybrid.

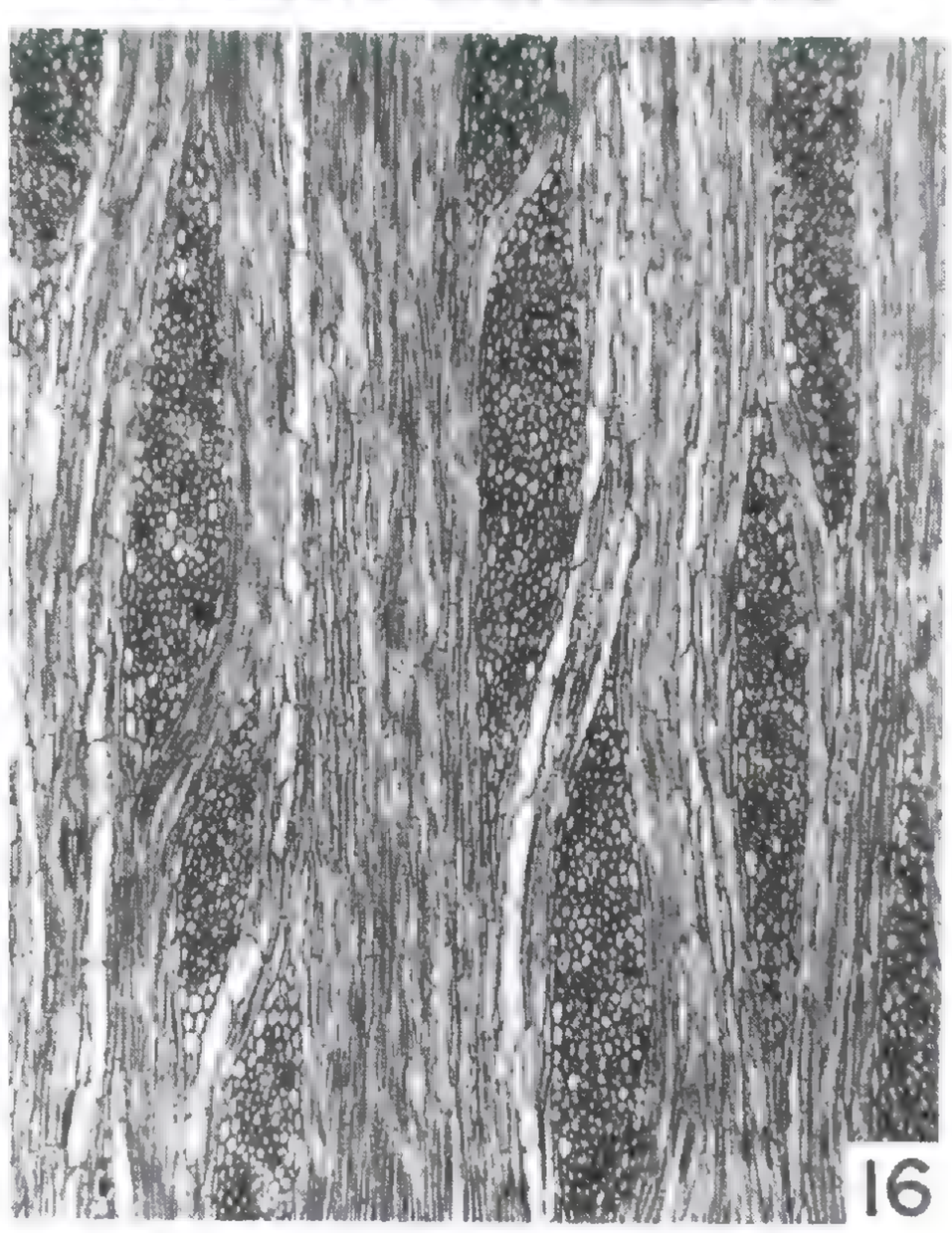
The species of *Scaevola* from Fiji to the Marquesas form a single phyletic series. Of these, *S. floribunda* of Fiji and *S. nubigena* of Samoa are most closely related to each other. *Scaevola floribunda* can become a tree to 6 meters, but *S. nubigena* and *S. marquesensis* are shrubs. A distinctive new species from Tahiti, *S. tahitensis,* is described in an accompanying paper (Carlquist, 1969); this species represents the first montane *Scaevola* to be reported between Savaii, Samoa, and the Marquesas Islands.

Most of the Hawaiian species of *Scaevola* are shrubs, but *S. glabra, S. gaudichaudiana,* and *S. "procera"* can be small trees, to about 5 meters. *Scaevola glabra* probably represents an early introduction of sect. *Scaevola* to the Hawaiian Islands. It exemplifies loss of dispersibility (Carlquist, 1966*a*) and adaptation to ornithophily (Carlquist, 1970*a*). However, there are no basic features in *S. glabra* alien to the fleshy-fruited species of *Scaevola*—curved flowers borne singly in an axillary fashion can be found in *S. indigofera* and Australian scaevolas; yellow flower color occurs in *S. gaudichaudii* (Gillett, 1969) and *S. tomentosa.* If *S. glabra* were recognized as a separate genus, *Camphusia* de Vriese, the genus *Scaevola* could with justification be broken into a number of genera. *Scaevola kauaiensis* is regarded here as a synonym of *S. glabra.*

The Hawaiian species other than *S. glabra* and *S. taccada* appear to represent a single phyletic series closely related to the series beginning with *S. montana* described above, although one or two further exceptions might be entertained. At any rate, *S. gaudichaudiana* and its close allies *(S. chamissoniana, S. mollis)* represent adaptations to wet forest. *Scaevola kilaueae* and *S. gaudichaudii* favor drier habitats. These two species tend not to be true upright shrubs, but are typically branched from near ground level. *Scaevola coriacea* is a sprawling species adapted to dry localities near the coast. It might be a derivative of the *S. gaudichaudiana* complex, but the possibility of a relationship to *S. plumieri,* which it resembles in a number of ways, ought to be investigated. Both *Scaevola gaudichaudiana* and *S. chamissoniana* can range from relatively wet to relatively dry forest; *S. gaudichaudiana* and *S. mollis,* a wet-forest species characteristically, hybridize. Such hybrids were termed *S. cerasifolia* by Skottsberg (1927). *Scaevola procera* of Hillebrand (1888) is probably a stabilized hybrid between these species. The nature of hybridization between *S. gaudichaudiana* and *S. mollis* has been analyzed excellently by Gillett (1966). The Hawaiian species *S. chamissoniana, S. gaudichaudiana,* and *S. mollis* are relatively weedy; this may be an indication of variability achieved at least in part by hybridization. *Scaevola gaudichaudii* (called *S. menziesiana* Cham. by Skottsberg) is a distinctive Hawaiian species, not to be confused with *S. gaudichaudiana. Scaevola gaudichaudii,* described well in habitat and morphology recently by Gillett (1969), has one-flowered cymes like the species of section *Crossotoma.* The nature of its relationships, whether to the *S. gaudi-*







FIGURES 13–16.— 13–14. *Dampiera brownii* (*Carlquist 1316*).—13. Transection, pith below. Note occlusion of vessels by unidentified substances.—14. Tangential section. Rays are wide, distortions in course of axial elements are evident.— 15–16. *Scaevola spinescens* (*Carlquist 914*).—15. Transection. Note narrowness of vessels, which are, however, numerous.—16. Tangential section. Rays are very wide and rather short. — Scale of magnification shown beside Fig. 1.

chaudiana complex or to species of *Crossotoma,* needs to be investigated. For illustrations and descriptions of ecological adaptations of the various Hawaiian species of *Scaevola,* the reader is referred to Carlquist (1970*a*).

Evolution of *Scaevola* on Pacific islands has featured both arborescence and entry into wet forest. The Hawaiian species represent not only these tendencies, but adaptation to drier areas as well. The succulent leaves of *S. coriacea* and *S. kilaueae* are external indicators of xeromorphy. On the other hand, the leathery, glabrous leaves of *S. glabra* represent a definite adaptation in leaf characteristics to rain forest—areas occupied by *S. glabra* receive more than 100 inches of rain per year. Succulence characterizes *Scaevola spinescens, S. plumieri,* and *S. taccada* leaves and can be called a response to halophytic ecology.

The wide variety of growth forms and ecological adaptations in the genus *Scaevola* make this genus, together with the other genera of Goodeniaceae, an interesting group for study of wood anatomy in relation to ecology. Are changes in ecological adaptation followed by (or accompanied by) changes in wood anatomy, and if so, what are these changes in wood anatomy? Can longer as well as shorter vessel elements evolve in such a group? Is the theory of paedomorphosis (Carlquist, 1962) relevant to wood evolution in Goodeniaceae? What is the nature of wood evolution in a primarily herbaceous group, and how does it differ from patterns in a truly woody group of dicotyledons? Questions like these seem best answered by study of groups such as Goodeniaceae.

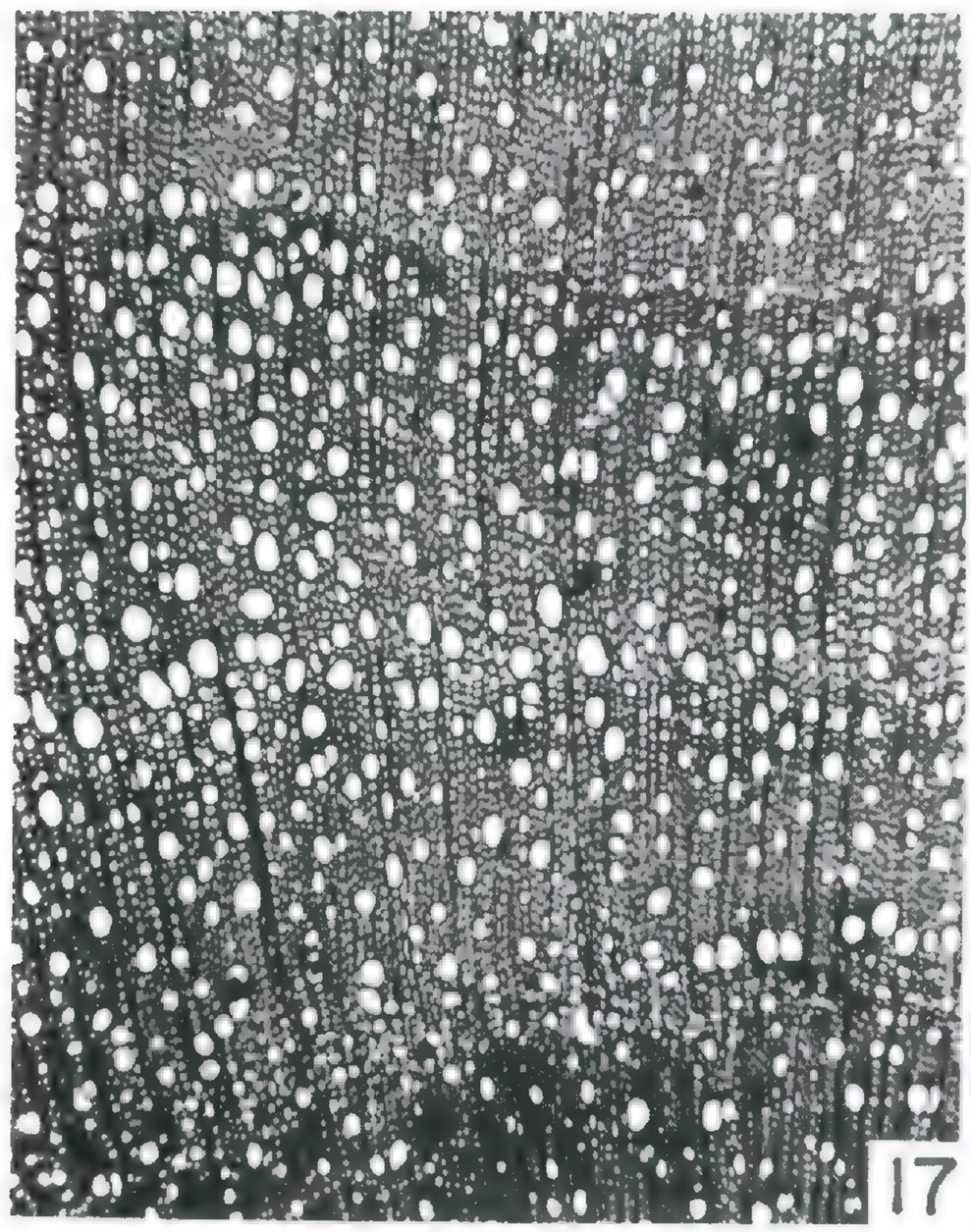
Data on wood anatomy of Goodeniaceae is extremely scanty. The description of wood for this family by Metcalfe and Chalk (1950) is derived almost exclusively from *S. taccada,* as those authors acknowledge. The data on wood anatomy of Goodeniaceae offered by Krause (1912) are insignificant. Kanehira (1921) described wood anatomy only for *S. taccada.* Data on vegetative anatomy other than wood were offered by Colozza (1908), Vesque (1876), Kienholz (1921), and Mullan (1931, 1933). Solereder (1885) summarized wood anatomy for the family, but his description is based on three species which are not identified with respect to particular features in his text, so his generalizations are not very useful. The only significant comparative wood study to date is that of Stern and Brizicky (1958), who analyzed wood of *S. plumieri* and compared it to wood of *S. taccada, S. gaudichaudiana,* and *S. floribunda.*

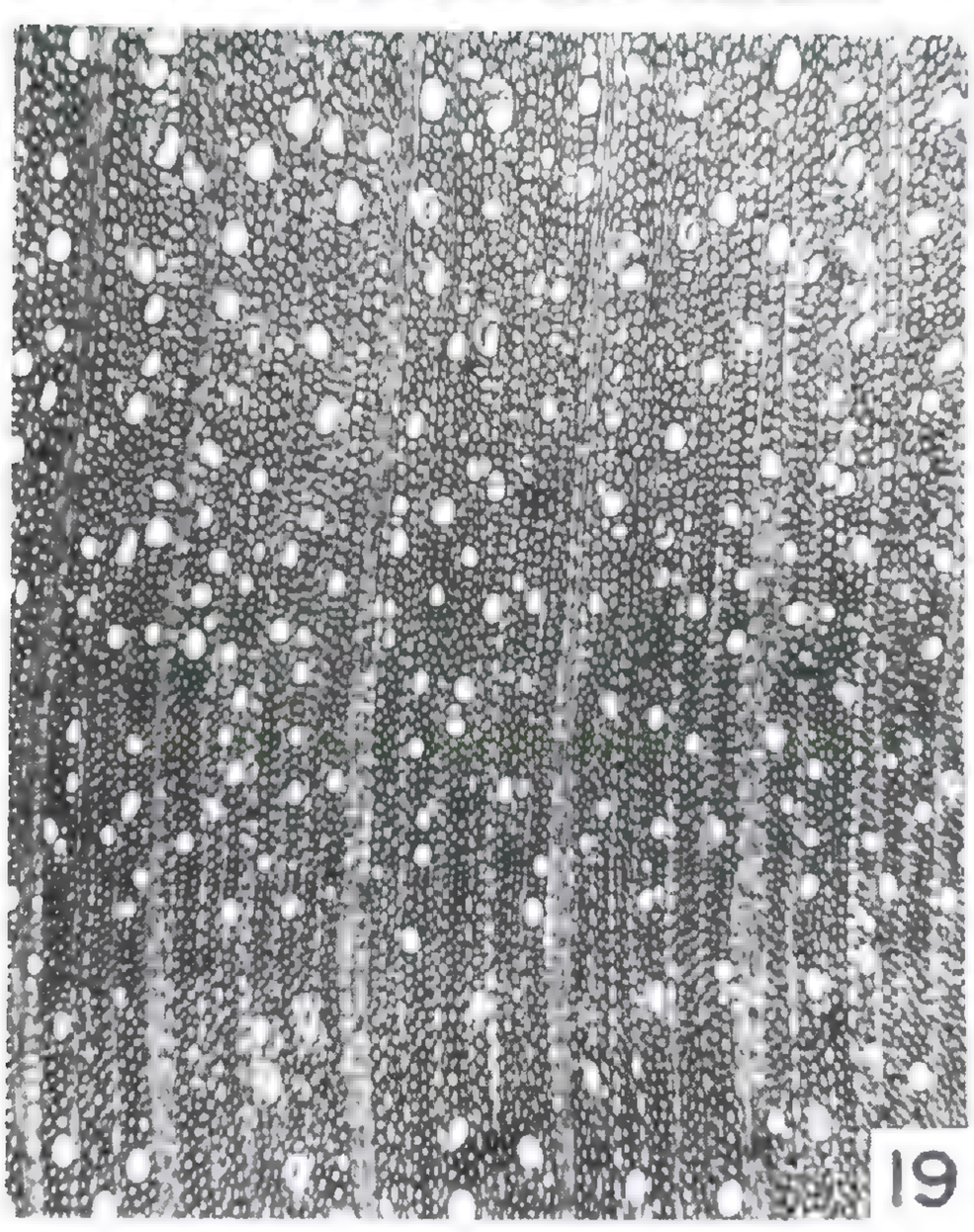
Materials, Methods, and Acknowledgments

Because woods of Goodeniaceae are virtually absent from institutional wood collections, most of the woods studied here had to be collected in the field. Some samples from the U.S. National Museum (USw) and the Arnold Arboretum (Aw) wood collections were available.

Many individuals have assisted my field work, and I wish to extend thanks particularly to Dr. William L. Stern and Dr. George W. Gillett. Others who deserve thanks for aid in my field work or in microtechnical tasks include Mrs. Jane Benjamin Baker, Mr. Norman Carlson, Mr. Alex George, the late Mr. Fred W. Humphreys and Mrs. Humphreys, Dr. Robert Jancey, Mr. Tim O. Magee, Mr. John Parham, Dr. Harold St. John, Prof. A. C. Smith, Dr. Robert F. Thorne, Miss Linda Thorne, and Mrs. Ann Platt Walker.

Wood samples were dried in the areas where they were collected. Wood samples of Goodeniaceae dry readily without molding, especially if bark is partly removed. Sections and macerations of the various samples were prepared using the usual techniques. The vessels, tracheids, and fiber-tracheids of many Goodeniaceae have what could be called a gelatinous





FIGURES 17–20.—Wood sections of Australian species of *Scaevola*. — 17 18. *Scaevola fasciculata* (*Carlquist 897*).—17. Transection. Several growth rings are evident.—18. Tangential section. Rays are narrow and inconspicuous. — 19 20. *Scaevola nitida* (*Carlquist 1047*). —19. Transection.—20. Tangential section. Rays are wider and more conspicuous; earlywood vessels are shown. — Scale of magnification shown beside Fig. 1.

nature. Although this is not pronounced in many species, it often causes difficulties in sectioning.

Features considered to show significant differences or similarities among the taxa are summarized in Table 1, and further explanation of symbols is given below. For quantitative data, 50 or more measurements per feature of each collection were taken. The diameter of fiber-tracheids and tracheids was obtained from measurement of these cells at their widest diameter (usually from a maceration) and averaging such measurements for each collection. The number of species and collections studied here is probably sufficient to give reliable results, at least in many characters of wood anatomy.

Anatomical Descriptions

The quantitative data in the table are self-explanatory. For qualitative data, symbols have been used.

ap = axial parenchyma more abundant at end of growth ring, or present only at end of growth ring.
bo = axial parenchyma present only in bands which represent the margin of a growth ring.
da = diffuse, relatively abundant.
ds = diffuse, relatively scanty.
ft = fiber-tracheids present, no tracheids.
mv = more numerous vessels at margin of growth ring.
t = tracheids present, no fiber-tracheids.
tft = both tracheids and fiber-tracheids present.
vs = vasicentric scanty.
wv = vessels wider at beginning of growth ring.
+ = feature present.
0 = feature absent.

With respect to ray histology, the letters indicate presence of cell types as seen in radial section: U = upright (erect); S = square; P = procumbent. Upper case indicates abundance of a cell type, lower case indicates paucity, and absence of the letter indicates no cells of a category could be found. Thus USP indicates abundance of upright, square, and procumbent cells; Us indicates upright cells abundant, with a few square cells and no procumbent cells.

VESSELS

Dimensions.—In Asteraceae, length and diameter of vessels in secondary xylem bears a very close relationship to degree of mesomorphy or xeromorphy (Carlquist, 1966*c*). Does this apply to Goodeniaceae as well? If we examine the data in Table 1 and arbitrarily designate average vessel-element length of more than 400μ as long and less than 200μ as short, we find a marked correlation with ecology. The rain forest species of *Scaevola* have long vessel elements almost without exception. Such long vessels are shown in Fig. 24, 26, 28, 34, and 36. Of the Goodeniaceae in which vessel-element length averages between 200μ and 300μ we find that all are xerophytes: *Coopernookia polygalacea* (Fig. 2), *C. strophiolata* (Fig. 4), *Dampiera glabrescens*, *Leschenaultia biloba* (Fig. 12), *L. floribunda*, *L. splendens* (Fig. 10), *Scaevola coriacea* (Fig. 30), *S. dielsii*, *S. holosericea*, *S. kilaueae*, *S. paludosa*, *S. spinescens* (Fig. 16), and *S. tomentosa*. To be sure, one

TABLE 1. Wood anatomy of Goodeniaceae. Specimens studied are listed under each taxon. See text for explanation of code below asterisk (*).

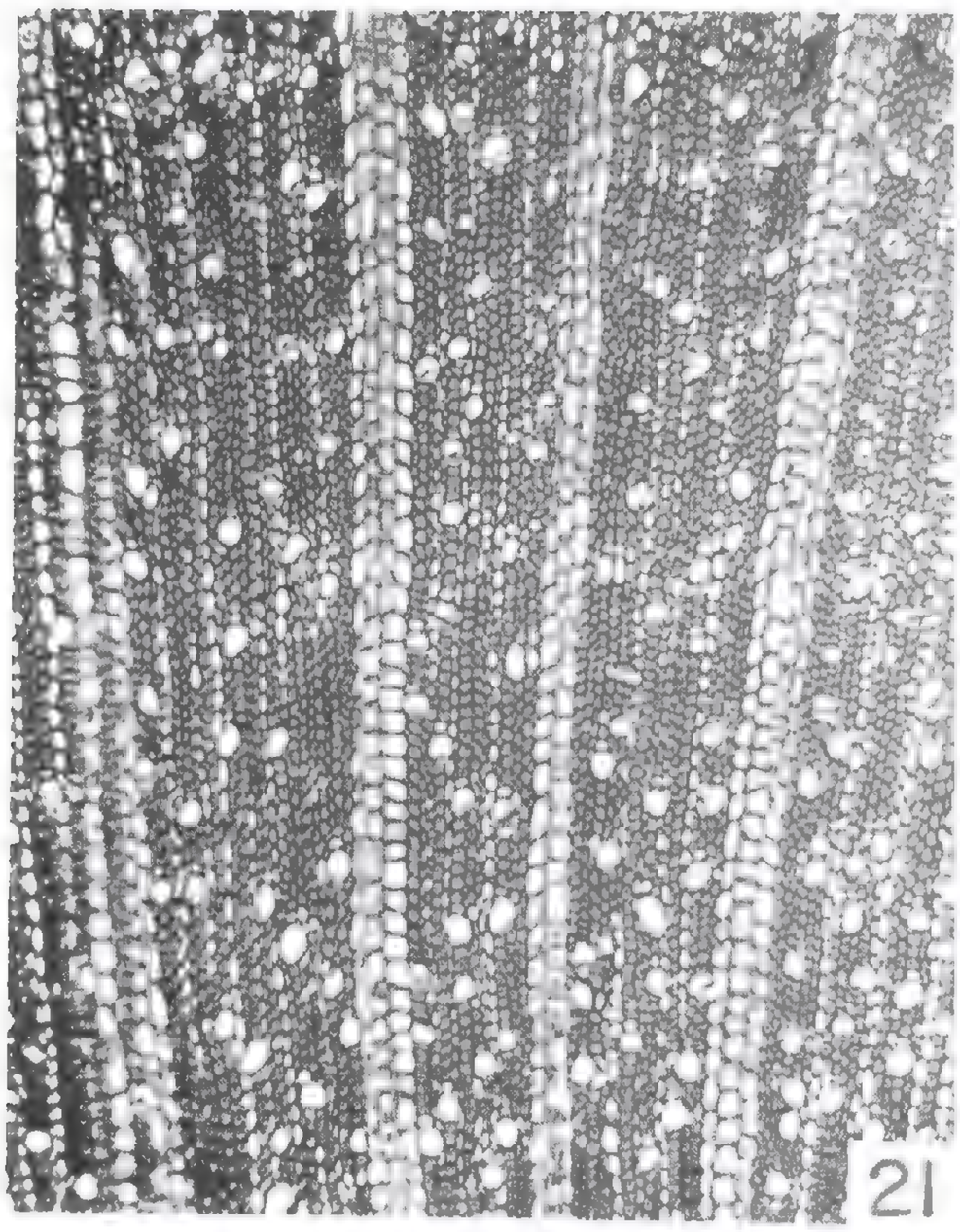
Taxon	Length Vessel Elements, Average, μ	Longest Vessel Element, μ	Vessel Diameter, Average, μ	Widest Vessel, μ	Vessels Per Group	Diameter Vessel Pits, μ	Length Tracheids or Fiber-Tracheids, Average, μ	Diameter Tracheids or Fiber-Tracheids, Average, μ	Thickness Walls Tracheids or Fiber-Tracheids, μ	Height Multiseriate Rays, Average, mm	Width Multiseriate Rays, Average, Cells	Ray Histology*	Axial Parenchyma*	Crystals	Growth Rings, Cells Distinguishing	Libriform Cell Types*
Coopernookia polygalacea (de Vriese) Carolin																
Carlquist 3475 (RSA)	210	357	29	49	1.4	4	370	17	5	1.0	4.2	uSP	bo	+	wv,ap	t
C. strophiolata (F. Muell.) Carolin																
Carlquist 3393 (RSA)	220	326	25	34	1.3	5	319	13	4	0.5	4.3	uSP	bo	+	wv,ap	t
Dampiera brownii F. Muell.																
Carlquist 1316 (RSA)	348	566	50	73	1.3	5	604	26	5	1.7	5.9	USp	bo	0	wv,ap	tft
D. glabrescens Benth.																
Carlquist 3041 (RSA)	248	367	34	49	1.1	4	382	18	6	0.8	4.5	USP	ds	0	0	t
Goodenia decurrens R.Br.																
Carlquist 1308 (RSA)	521	754	35	62	1.6	4	648	24	4	1.0	7.7	USp	bo	0	wv,ap	t
G. ovata J. E. Smith																
Carlquist 831 (RSA)	425	632	47	62	2.1	3	622	29	5	2.9	6.0	USp	da	0	0	tft
G. scapigera R.Br.																
Carlquist 3489 (RSA)	323	490	32	55	1.3	4	476	19	5	1.0	3.5	USp	ds	0	0	tft
Leschenaultia biloba Lindl.																
Carlquist 911 (RSA)	240	418	32	57	1.9	6	719	28	4	1.2	2.5	USp	bo	0	wv,ap	ft
L. floribunda Benth.																
Carlquist 881 (RSA)	236	383	37	57	2.0	5	559	25	2	0.8	4.6	USP	0	0	0	ft
L. splendens Hook.																
Carlquist 3437 (RSA)	269	449	34	52	1.4	4	386	19	4	rayless			0	0	0	t
Scaevola beckii Zahlbruckner																
Carlquist 705 (RSA)	651	963	38	53	2.4	3	956	25	6	0.7	2.9	USP	vs	+	wv	ft
Carlquist 723 (RSA)	561	882	33	57	3.0	4	927	27	6	1.0	3.1	USP	vs	+	wv	ft
S. chamissoniana Gaud. var. *bracteosa* Hillebr.																
Carlquist 614 (RSA)	295	398	76	107	1.2	5	698	29	3	1.8	5.3	USP	ds	0	0	tft

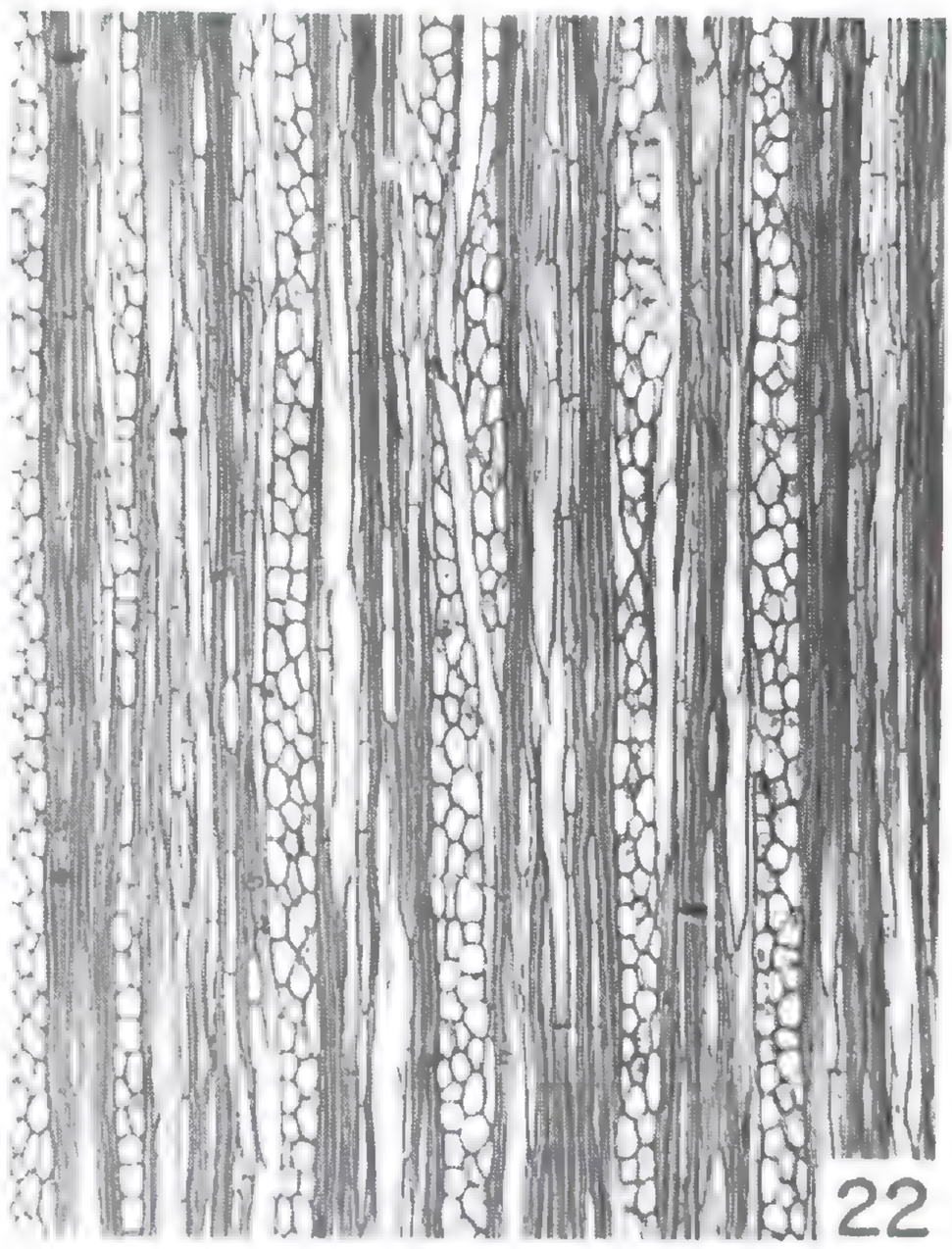
S. c. var. *chamissoniana*																	
Carlquist 1856 (RSA)	418	557	79	107	1.0	7	810	33	5	0.9	3.4	USP	ds	0	0	tft
Carlquist 2241 (RSA)	426	638	84	112	1.1	5	817	23	5	1.1	6.1	USP	ds	0	0	tft
S. c. var. *cylindrocarpa* (Hillebr.) Krause																	
Carlquist 2000 (RSA)	388	538	91	135	1.3	4	791	22	4	3.5	10.1	USP	ds	0	0	tft
S. coriacea Nutt.																	
Gillett 1561 (BISH)	233	406	57	103	1.3	3	324	22	4	1.4	5.3	USp	da	+	0	t
Carlquist 2125 (RSA)	260	381	90	160	1.7	5	409	25	4	1.1	4.7	USp	da	+	0	t
S. crassifolia Labill.																	
Carlquist 1015 (RSA)	302	429	64	82	1.7	4	463	24	3	1.9	5.8	USP	da	+	ap	t
Carlquist 3764 (RSA)	377	561	52	83	1.2	4	557	20	3	0.6	3.2	USP	da	+	ap	t
S. dielsii E. Pritz.																	
Carlquist 1028 (RSA)	296	433	44	57	1.0	3	388	21	5	0.7	5.0	USP	bo	+	wv,ap	t
S. fasciculata Benth.																	
Carlquist 897 (RSA)	422	246	38	68	1.3	6	522	23	5	0.9	2.0	USP	bo	0	ap	t
S. floribunda A. Gray																	
Carlquist 700 (RSA)	507	840	93	125	1.2	5	1099	27	6	3.0	6.6	Usp	da	0	0	ft
Aw-910	426	585	66	135	1.0	5	720	48	5	0.4	2.0	USp	da	0	0	ft
S. gaudichaudiana Cham.																	
Carlquist 578 (RSA)	411	667	56	90	1.0	7	717	30	4	2.6	6.2	USP	ds	0	0	ft
Carlquist 581 (RSA)	393	585	70	103	1.3	5	611	35	5	1.0	4.2	USP	ds	0	0	ft
Gillett 1404 (BISH)	500	690	54	70	1.3	6	883	28	4	0.9	3.8	USP	ds	0	0	ft
USw-15331	448	527	64	90	1.5	5	810	34	5	1.3	7.5	USP	ds	0	0	ft
USw-15333	466	620	82	111	1.2	5	880	36	5	1.0	4.1	USP	ds	0	0	ft
S. gaudichaudii H. & A.																	
Carlquist 2380 (RSA)	303	504	54	75	1.2	3	712	20	6	1.2	5.3	USP	vs,ds	+	0	ft
Munro 74 (BISH)	315	456	46	70	1.0	4	466	27	6	1.1	3.0	USP	vs,ds	+	0	ft
S. glabra H. & A.																	
Carlquist 506 (RSA)	403	772	65	103	1.4	7	1104	40	7	13.2	11.8	Usp	da	0	0	ft
Carlquist 1752 (RSA)	480	632	63	88	1.5	7	894	30	11	4.2	5.7	Usp	da	0	0	ft
Carlquist 1975 (RSA), near pith	533	918	90	143	1.5	9	1026	31	11	12.9	12.1	Usp	da	0	0	ft
Carlquist 1975 (RSA), outside base	359	616	74	107	1.4	6	1065	30	11	3.1	7.0	Usp	da	0	0	ft
Stern & Carlquist 1247 (US, RSA)	454	889	68	98	1.8	9	1168	36	7	8.9	8.8	USp	da	0	0	ft
S. holosericea de Vriese																	
Carlquist 1027 (RSA)	268	374	63	103	1.6	4	404	24	3	1.5	7.4	sP	ds	+	0	t

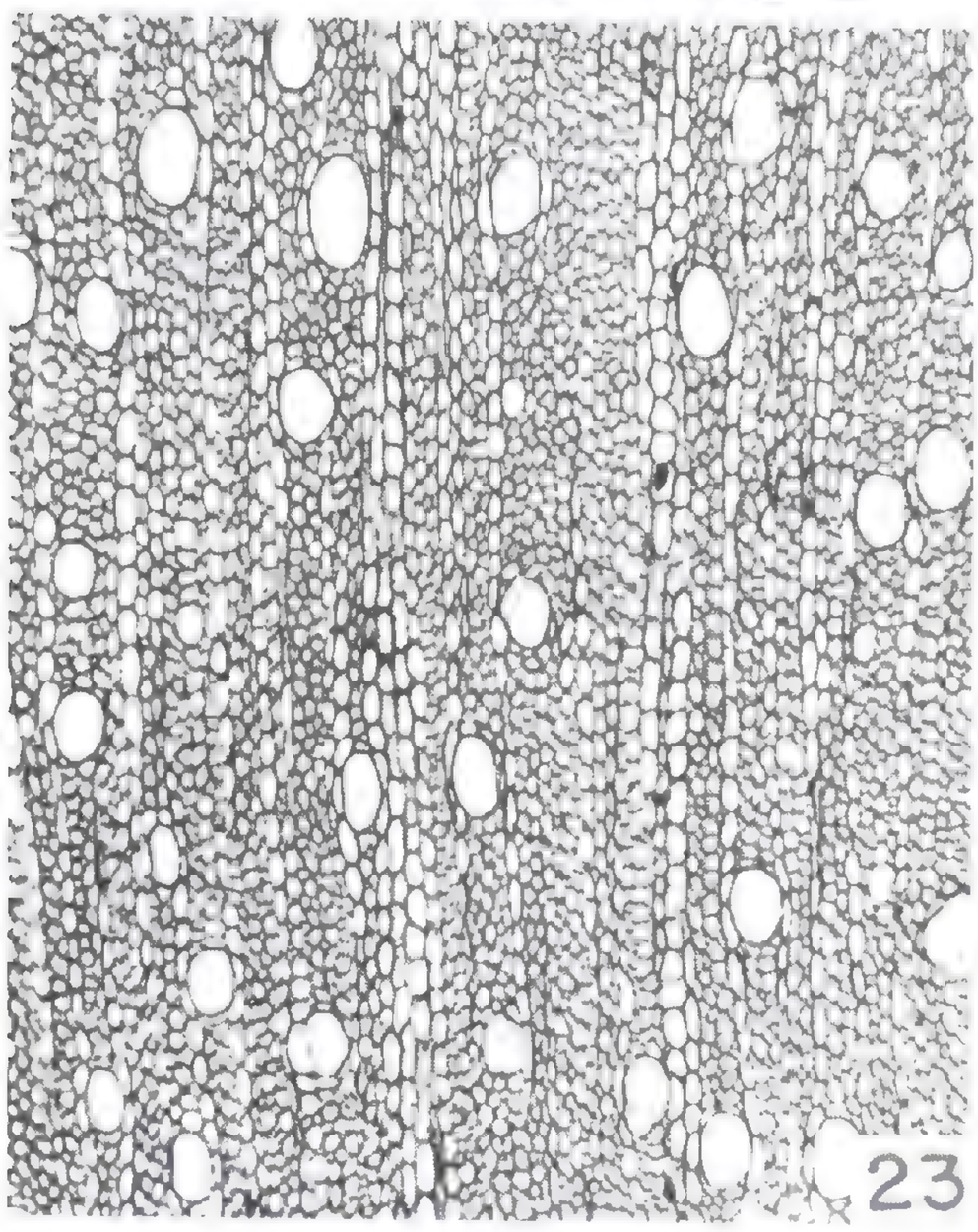
TABLE 1. Wood anatomy of Goodeniaceae. Specimens studied are listed under each taxon. See text for explanation of code below asterisk (*). Continued from page 371.

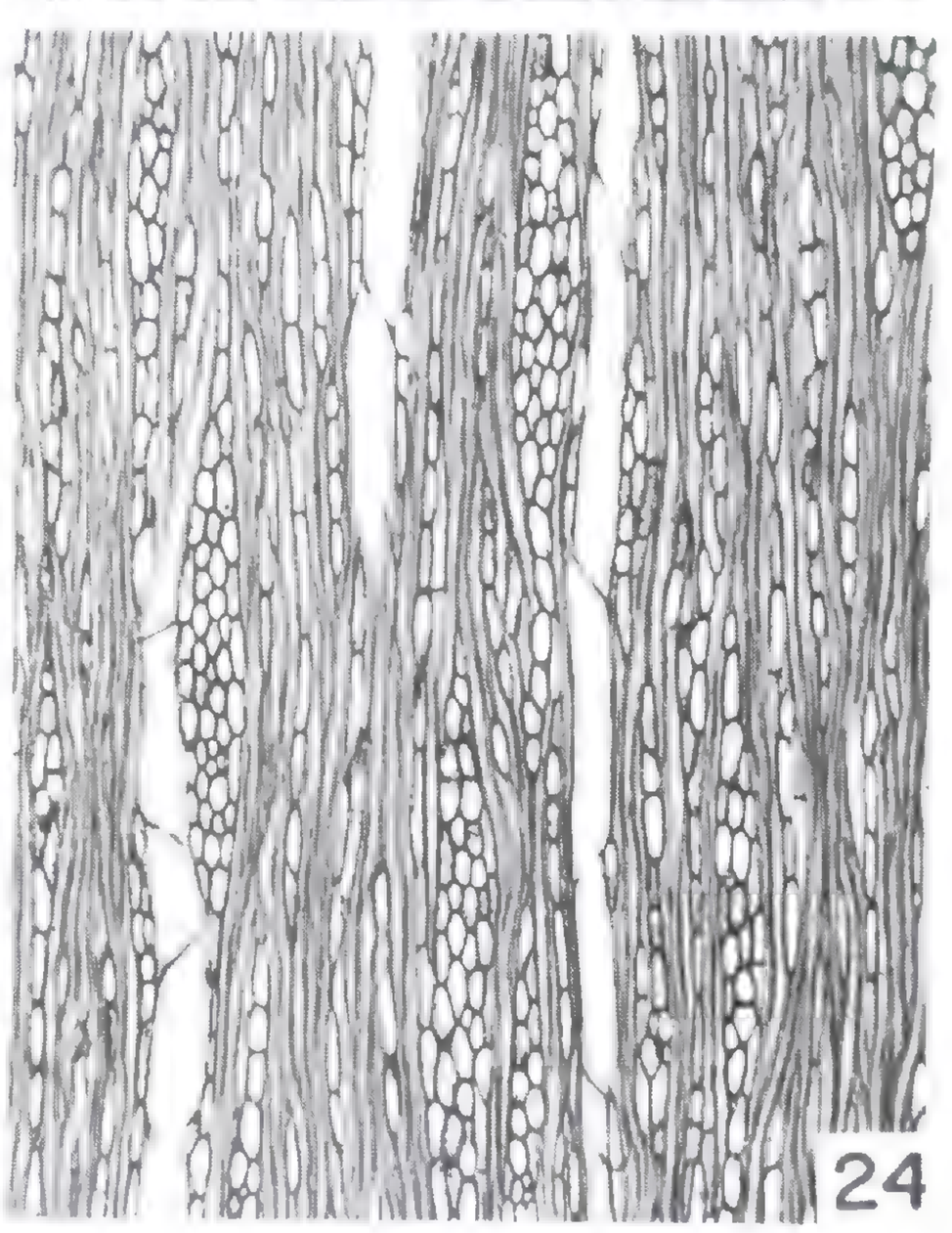
Taxon	Length Vessel Elements, Average, μ	Longest Vessel Element, μ	Vessel Diameter, Average, μ	Widest Vessel, μ	Vessels Per Group	Diameter Vessel Pits, μ	Length Tracheids or Fiber-Tracheids, Average, μ	Diameter Tracheids or Fiber-Tracheids, Average, μ	Thickness Walls Tracheids or Fiber-Tracheids, μ	Height Multiseriate Rays, Average, mm	Width Multiseriate Rays, Average, Cells	Ray Histology*	Axial Parenchyma*	Crystals	Growth Rings, Cells Distinguishing	Libriform Cell Types*
S. indigofera Schl.																
Carlquist 736 (RSA)	527	831	71	107	1.0	7	1005	28	3	1.7	4.2	USp	ds	0	0	ft
Carlquist 781 (RSA)	456	620	73	107	1.2	4	1005	29	5	1.1	4.0	USp	ds	0	0	ft
Carlquist 801 (RSA)	475	737	87	115	1.5	5	1052	33	7	1.3	3.9	USP	ds	0	0	ft
S. indigofera Schl. × *S. montana* Labill.																
Carlquist 734 (RSA)	461	632	128	156	1.2	6	1024	40	6	0.9	4.1	USP	ds	0	0	tft
Carlquist 803 (RSA)	407	585	111	160	1.2	6	1003	34	6	1.0	3.7	USp	ds	0	0	ft
S. kilaueae Degener																
Carlquist 2050 (RSA)	225	403	67	95	1.2	4	550	23	5	2.7	7.8	usP	ds,vs	+	wv	t
S. mollis H. & A.																
Carlquist 574 (RSA)	411	585	53	90	1.0	3	589	31	4	1.0	4.9	USP	ds	0	0	ft
Carlquist 1601 (RSA)	408	562	68	94	1.2	5	785	26	5	0.8	5.6	USP	ds,vs	0	0	ft
Carlquist 1674 (RSA)	434	620	64	102	1.2	6	757	28	3	1.4	4.6	USP	ds	0	0	ft
S. montana Labill.																
Carlquist 710 (RSA)	414	655	99	156	1.0	7	705	37	4	1.4	4.1	Usp	da	0	wv	ft
Carlquist 714 (RSA)	321	655	76	115	1.3	3	840	28	4	1.6	5.0	USp	da	0	0	ft
Carlquist 715 (RSA)	624	948	70	98	1.4	3	977	27	4	1.7	4.3	Usp	da	0	wv	ft
Carlquist 716 (RSA)	359	491	60	82	1.1	3	692	28	4	1.8	4.9	USp	da	0	wv	ft
Carlquist 717 (RSA)	407	620	75	102	1.6	3	713	27	4	1.5	4.0	Usp	da	0	0	ft
Carlquist 749 (RSA)	491	831	94	135	1.1	6	1102	28	5	1.4	3.8	USp	da	0	0	ft
S. nitida R. Br.																
Carlquist 1047 (RSA)	393	562	52	82	1.1	3	749	28	5	0.9	4.4	USp	ds	+	wv	ft
S. oppositifolia Roxb.																
Carlquist 1386 (RSA)	489	840	91	160	1.3	3	1250	31	6	4.0	?	USP	da	+	0	ft

S. paludosa R. Br.																
Carlquist 880 (RSA)	229	503	51	78	1.9	5	580	21	3	4.4	6.6	USP	bo	+	ap	t
S. platyphylla Lindl.																
Carlquist 3586 (RSA)	417	847	35	47	1.3	4	559	18	5	10.5	8.2	Us	bo	+	ap	tft
S. plumieri (L.) Vahl																
W. G. Earle, s. n. (US)	376	562	101	123	1.8	4	701	31	5	1.8	4.6	USp	vs	0	0	tft
Stern & Brizicky 289 (US)	296	502	107	164	1.0	5	388	30	4	1.5	4.8	USp	vs	0	0	tft
S. porocarya F. Muell.																
Carlquist 2957 (RSA)	428	663	43	78	1.2	4	721	22	6	4.8	5.3	usP	bo	+	ap	ft
S. "procera Hillebr."																
Carlquist 515 (RSA)	305	468	81	111	1.4	5	530	30	3	0.7	4.5	USP	ds	0	0	ft
Stern & Carlquist 1235 (US, RSA)	380	585	80	115	1.0	5	826	32	4	0.8	4.6	USP	ds	0	0	ft
S. sericophylla F. Muell.																
Carlquist 2986 (RSA)	497	887	44	83	1.1	4	652	15	4	0.8	3.5	Usp	bo	–	ap	tft
S. spinescens R. Br.																
Carlquist 914 (RSA)	234	328	47	68	1.7	3	696	23	6	2.1	8.1	uSP	da	–	ap	ft
S. taccada (Gaertn.) Roxb.																
E. H. Bryan, Jr., s. n. (BISH)	338	468	89	144	1.5	7	480	29	5	4.4	5.6	Us	vs	0	0	tft
Carlquist 573 (RSA)	344	562	96	123	1.2	7	470	31	3	1.8	10.8	Us	vs	0	0	tft
Carlquist 701 (RSA)	388	620	103	148	1.0	10	1110	34	4	1.9	7.0	Us	vs	0	0	tft
Carlquist 775 (RSA)	310	491	89	111	1.0	6	739	28	4	1.5	7.1	Usp	vs	0	0	tft
Carlquist 801 (RSA)	415	527	96	144	1.0	6	1155	35	4	2.0	5.1	Us	vs,ds	0	0	tft
Carlquist 1264 (RSA)	398	562	134	193	1.0	7	531	30	4	2.5	6.0	Us	vs,da	0	0	tft
Carlquist 1407 (RSA)	463	667	86	144	3.1	7	1199	31	5	0.7	3.2	Us	vs	0	0	tft
USw-12022	428	538	107	152	1.1	5	1021	33	4	2.3	6.1	Us	vs	0	0	tft
USw-15330	381	550	109	139	1.2	7	510	32	4	2.1	10.2	Us	vs,ds	0	0	tft
S. tahitensis S. Carlquist																
Carlquist 654 (RSA)	441	573	73	119	1.5	6	741	26	5	2.6	5.1	Usp	ds	0	0	ft
S. tomentosa Gaud.																
Carlquist 2954 (RSA)	237	377	47	60	1.2	4	535	20	6	1.8	9.9	usP	ds	+	ap,mv	tft
Verreauxia reinwardtii (De Vriese) Benth.																
Carlquist 878 (RSA)	324	527	37	59	1.1	6	672	22	5	1.1	4.2	USP	0	0	0	t
Carlquist 2894a (RSA)	355	536	47	73	1.3	5	500	21	6	0.7	4.1	USP	0	0	0	t









FIGURES 21–24.—Wood sections of New Caledonian species of *Scaevola*. — 21–22. *Scaevola beckii (Carlquist 705)*.—21. Transection. Note narrow vessels and thick-walled tracheids. —22. Tangential section. Rays are tall. — 23–24. *Scaevola montana (Carlquist 714)*.—23. Transection. Note wide vessels.—24. Tangential section. Rays large-celled and conspicuous. — Scale of magnification shown beside Fig. 1.

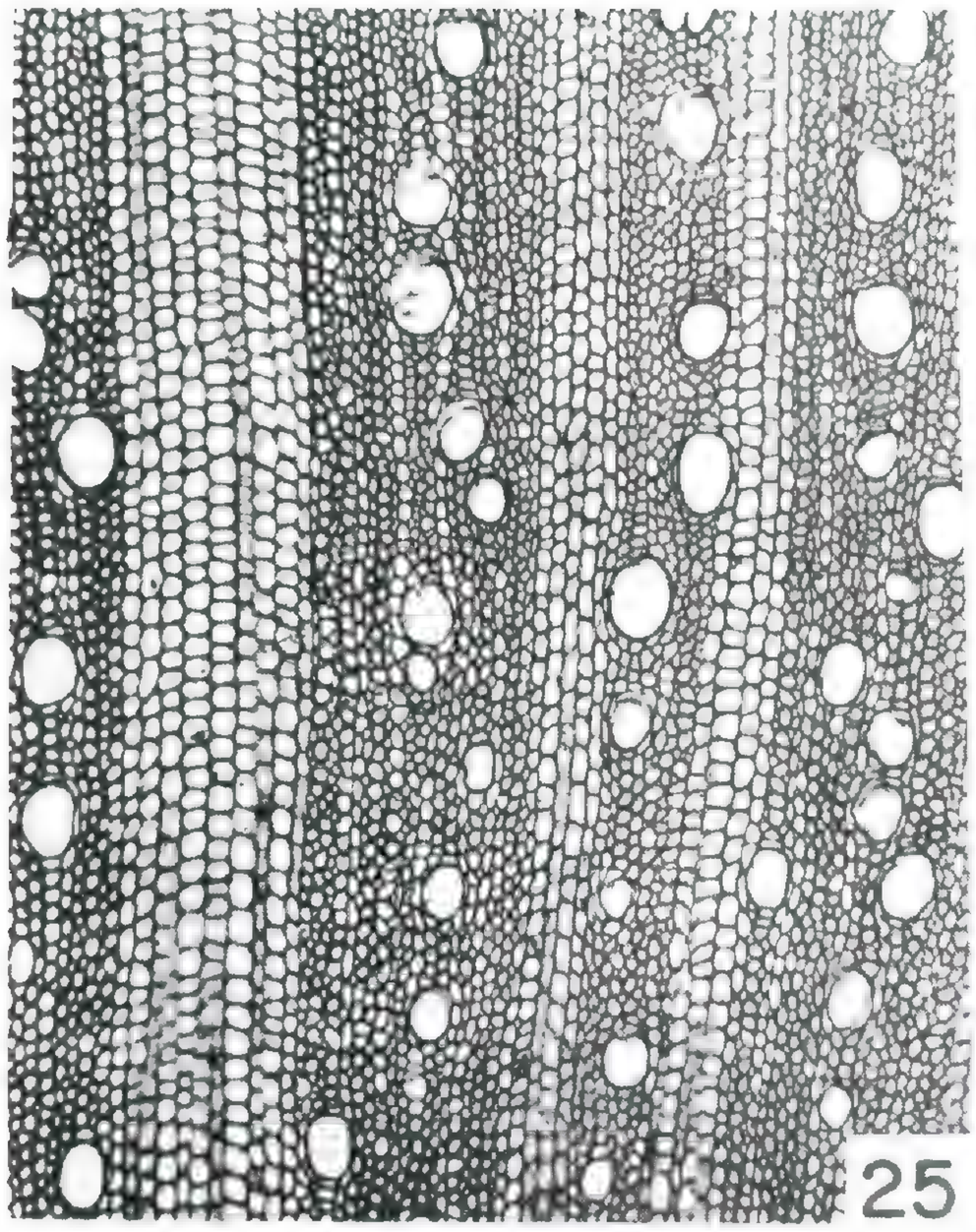
finds some species in which vessel elements do not, at first, seem to agree with this distinction between xeromorphy and mesomorphy. *Goodenia decurrens* has relatively long vessel elements, but this is a short-lived perennial of moderately wet forest in which growth takes place during spring months when water is available. This might also be true of *Scaevola platyphylla, S. sericophylla,* and possibly *S. beckii* (Fig. 22). Relatively long vessel elements occur in most collections of *S. taccada* (Fig. 40) and *S. plumieri* (Fig. 38) as well as in *S. porocarya. Scaevola taccada* seems paradoxical in this respect, for we would expect a halophyte to be a xeromorph at first glance. However, *S. taccada* might qualify as a succulent, and succulent species appear to exemplify paedomorphosis or perhaps actual mesomorphy.

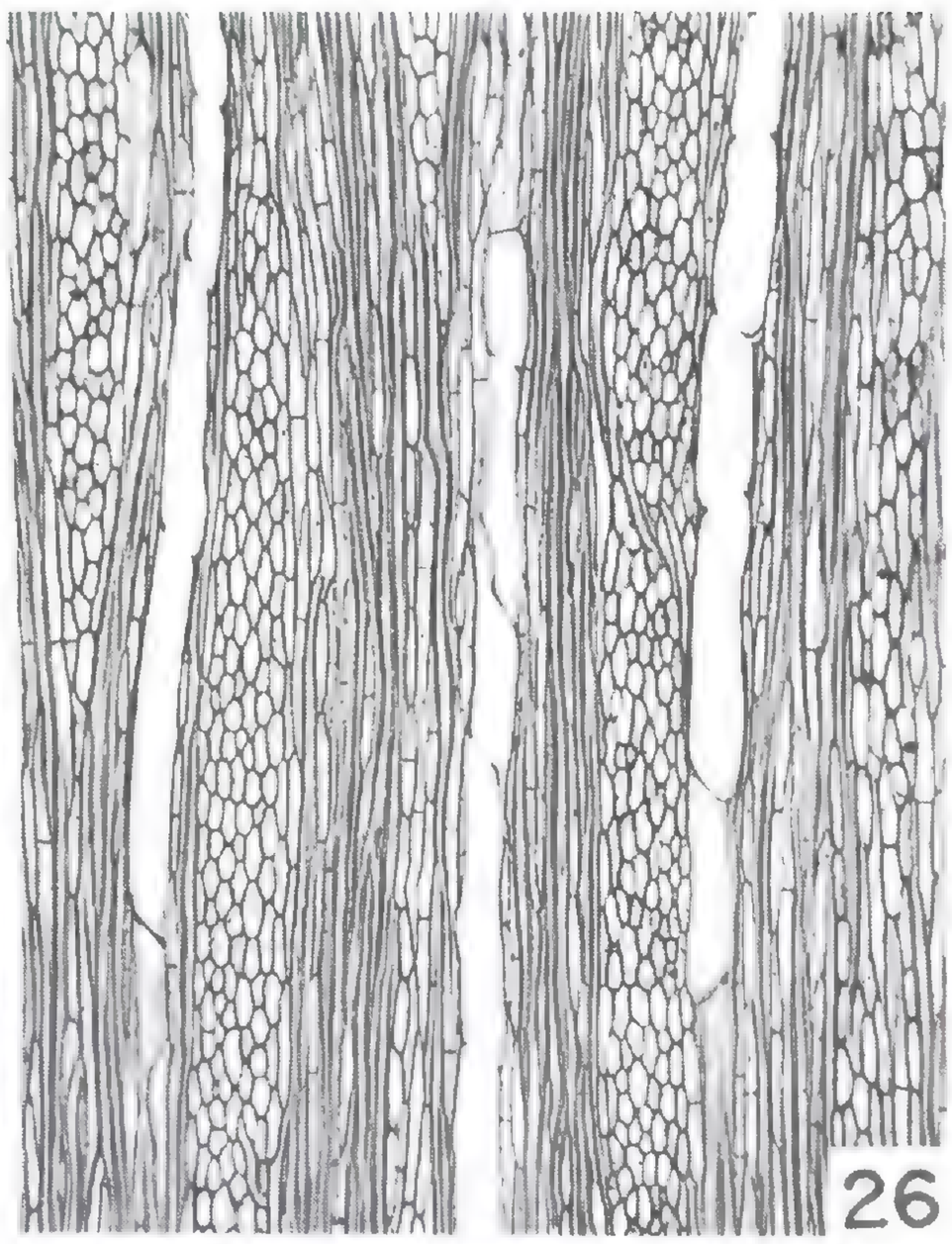
With respect to vessel diameter, trends of xeromorphy and mesomorphy are even clearer than they are with vessel-element length. Thus, narrow vessel diameter characterizes the species of dry habitats: *Coopernookia polygalacea* (Fig. 1), *C. strophiolata* (Fig. 3), *Leschenaultia biloba*(Fig. 11), *L. floribunda, L. splendens* (Fig. 9), *Scaevola beckii* (Fig. 21), *S. fasciculata* (Fig. 17), *S. nitida* (Fig. 19), *S. paludosa, S. platyphylla, S. porocarya, S. sericophylla, S. spinescens* (Fig. 15), and *S. tomentosa.* The montane insular species of *Scaevola* have relatively wide vessels (Fig. 23, 25, 27, 33, 35). The only Australian Goodeniaceae to have relatively wide vessels are from wet forest: *Goodenia ovata* (Fig. 5) and *Scaevola oppositifolia* (Fig. 41). Wide vessels in *S. oppositifolia* probably relate not only to this, but to the scandent habit of that species. This factor very likely applies also to *S. coriacea* (Fig. 29), which could be described as a prostrate non-twining vine. On the basis of vessel diameter, *S. plumieri* (Fig. 37) and *S. taccada* (Fig. 39) ought to qualify as mesic. Perhaps these succulent or semi-succulent seaside shrubs, like comparably succulent species of *Euphorbia* (Carlquist, 1970*b*), can be said to have a mesic *internal* environment in their stems.

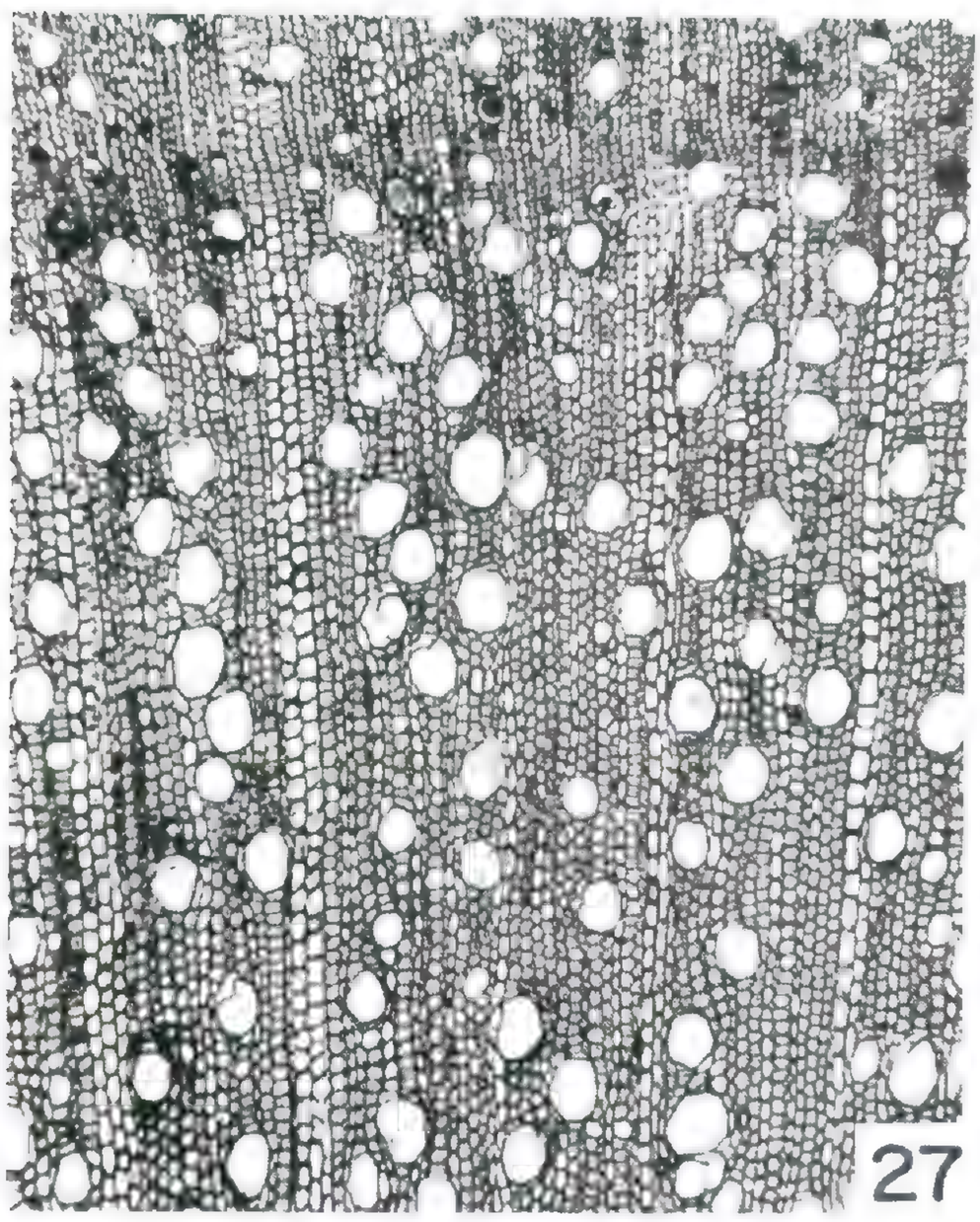
Abundance.—Metcalfe and Chalk (1950) claim absence of vessels from *Scaevola spinescens.* This is, as noted by Stern and Brizicky (1958), a mistranslation of Krause's (1912) statement that vessels are almost absent. Krause's statement, in turn, is copied from a footnote in a paper by Vesque (1876). However, Vesque may have been confused by the narrow vessels in *S. spinescens* (Fig. 15, 16); in fact, vessels are exceptionally abundant in this species.

In general, Goodeniaceae show vessel abundance in inverse proportion to vessel diameter. Because I selected the latter measure, data on vessel abundance was not presented here.

Perforation Plates.—Goodeniaceae have basically simple perforation plates. Scalariform perforation plates, mixed with simple ones, were reported for *Scaevola plumieri, S. taccada,* and *S. gaudichaudiana* by Stern and Brizicky (1958). Such a condition also occurs in *Goodenia ovata, Scaevola mollis, S.montana,* and *S. "procera."* More species could undoubtedly be added to this list by more intensive observation. The occurrence of such plates has been interpreted as a vestige of a primitive condition by Stern and Brizicky (1958). However, in the species where scalariform perforation plates occur, most plates are simple and the scalariform plates (which generally have 10–15 bars) are definitely in the minority. Many of







FIGURES 25–28.—Wood sections of Fijian and Tahitian species of *Scaevola*. — 25 26. *Scaevola floribunda* (*Carlquist 700*).—25. Transection. Note wide vessels.—26. Tangential section. Rays are wide and tall. — 27–28. *Scaevola tahitensis* (*Carlquist 654*).—27. Transection. Note thick-walled fiber-tracheids.—28. Tangential section. Ray cells are mostly upright. — Scale of magnification shown beside Fig. 1.

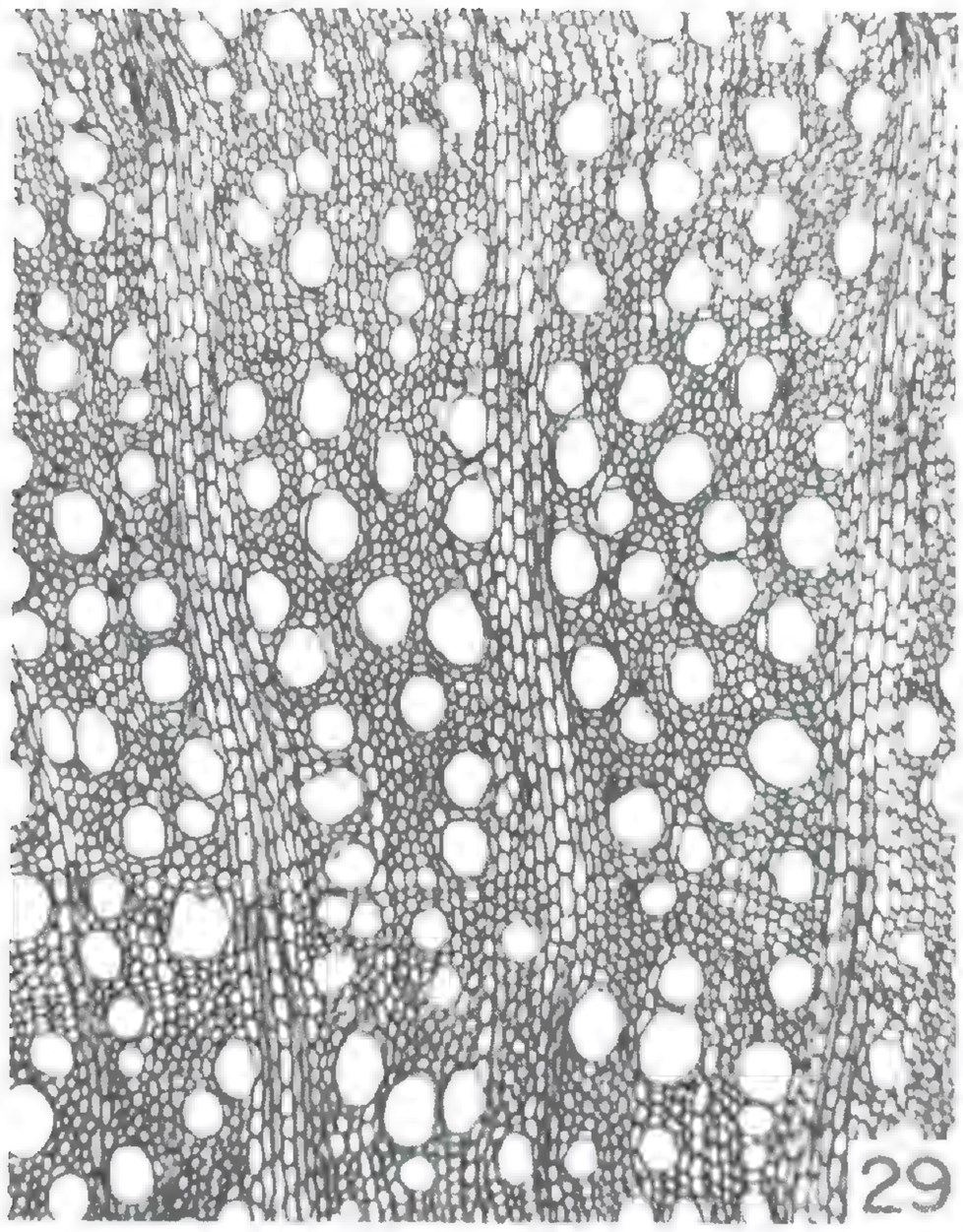
the scalariform plates, where present, have aberrant structure with anastomosing and variously-oriented bars. If scalariform plates were present as a vestige, one would expect them to be in the majority, and if simple plates were also present, all grades of transition from many to few bars ought to occur. This does not appear to characterize any Goodeniaceae. Occurrence of scalariform perforation plates does not appear to be an indicator of primitiveness in Cichorieae (Carlquist, 1960*a*). In that group these plates are not common and tend to occur only in mesomorphic species. This appears to be true in Goodeniaceae also.

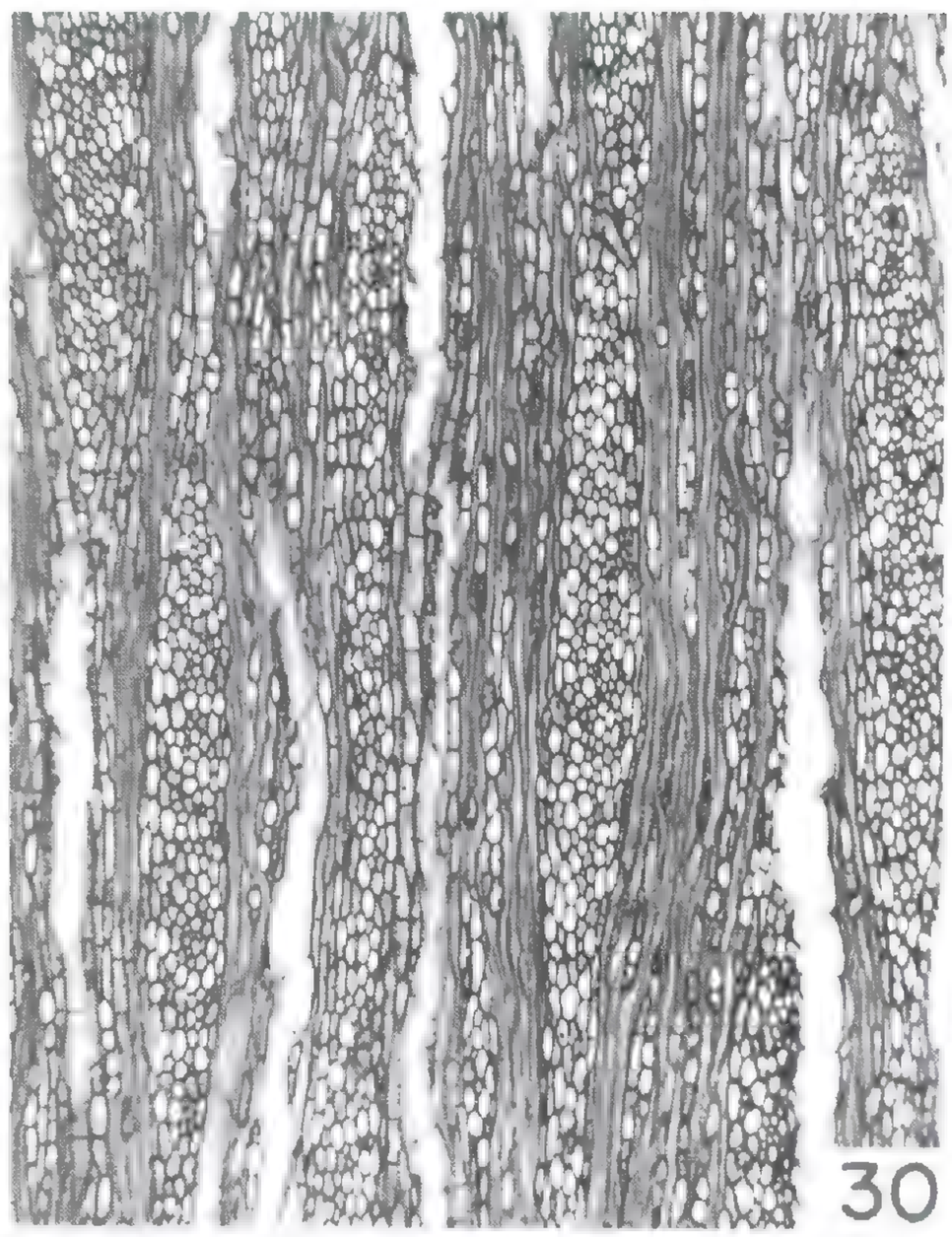
Lateral-Wall Pitting.—The presence of scalariform lateral-wall pitting in a group with the characteristics of Goodeniaceae seems more an indicator of juvenilism than of primitiveness. *Scaevola glabra* (Fig. 45) exemplifies this pitting condition more clearly than any other Goodeniaceae and was cited in this regard earlier (Carlquist, 1962). However, other species of *Scaevola* also show scalariform or transitional pitting. Vessels of *S. chamissoniana* var. *chamissoniana* (Fig. 44) show scalariform vessel-parenchyma pitting but also show, in part, this type in areas of intervascular pitting. Such a scheme of lateral-wall pitting was also observed in *S. floribunda, S. gaudichaudiana, S. kilaueae, S. mollis, S. montana,* and *S. tahitensis.* Stern and Brizicky (1958) listed "alternate and transitional" pitting for intervascular areas of vessels in *S. gaudichaudiana.* This list of species suggests that wet-forest species are most likely to have scalariform or transitional lateral-wall pitting. This also proved to be the case in another genus of dicotyledons that has adapted to wet forest in the Hawaiian Islands, *Euphorbia* (Carlquist, 1970*b*).

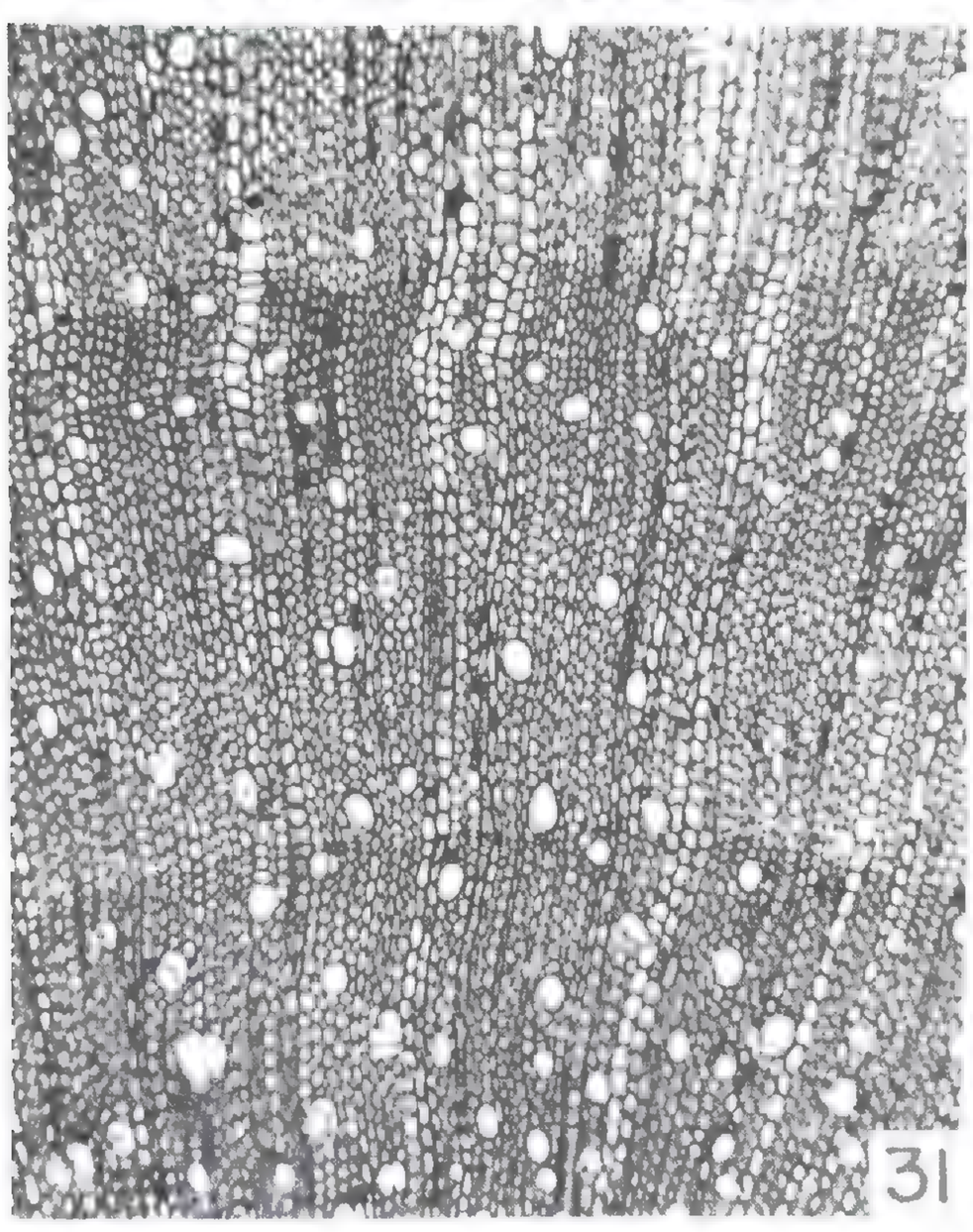
Scalariform or transitional intervascular pitting also occurs in *S. taccada* and, to a limited extent, *S. plumieri,* as noted by Stern and Brizicky (1958). If the longer, wider vessels in these two species are indications of mesomorphy or succulence or paedomorphosis (concepts closely interrelated), then this pitting type in these species is understandable. This appeared to be true in insular species of *Euphorbia* (Carlquist, 1970*b*). Vegetative portions of *Scaevola taccada* and *S. plumieri* are certainly succulent, as shown by Kienholz (1921) and Mullan (1931, 1933).

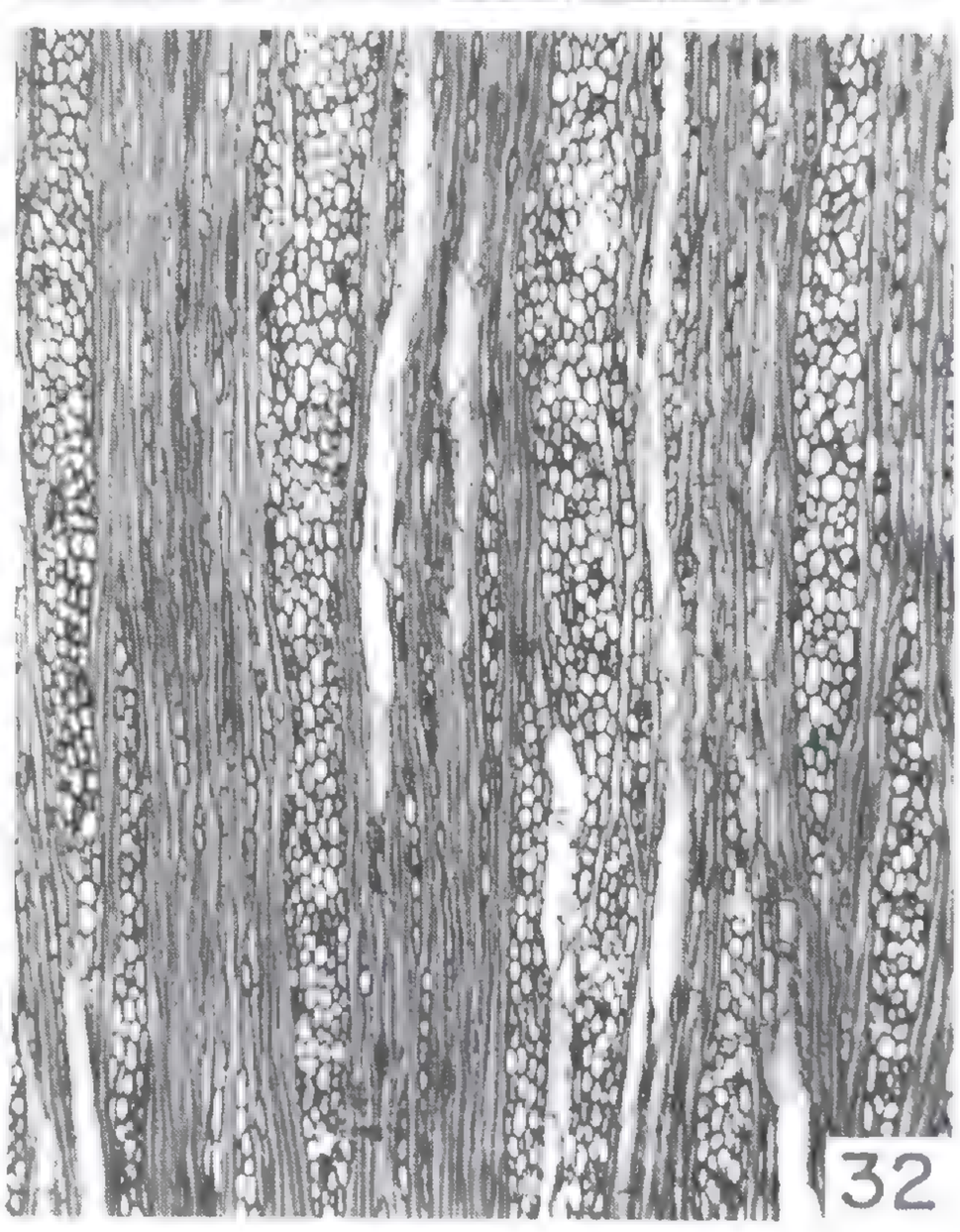
Xeromorphy appears to be basic to other vessel-wall modifications. The species of Goodeniaceae not listed above may be assumed to have alternate pitting exclusively or nearly so. However, a few of these show, in addition, occurrence of grooves or bands. Vessel pits in which the pit apertures are elongate, forming short grooves to either side of a pit, were observed in *Dampiera glabrescens, Scaevola nitida,* and *S. oppositifolia.* More marked grooves, which tend to interconnect several apertures in a helix on the vessel wall, were observed in *S. beckii, S. coriacea,* and *S. spinescens* (Fig. 43). *Scaevola spinescens* has the most conspicuous grooves in this series. A species closely allied to *S. spinescens, S. tomentosa,* lacks grooves, however. *Scaevola tomentosa* is a less xeromorphic species than *S. spinescens.*

The two species of *Coopernookia* exhibit a more marked form of xeromorphy—presence of fine bands, the so-called "tertiary helical thickenings" of some authors. This condition is illustrated for *C. polygalacea* (Fig. 42). *Coopernookia* wood qualifies as the most xeromorphic of Goodeniaceae on the basis of vessel dimensions.









FIGURES 29–32.—Wood sections of lowland Hawaiian species of *Scaevola*. — 29 30. *Scaevola coriacea (Carlquist 2125)*.—29. Transection. Note the rather wide vessels; these are probably related to the sprawling habit of the plant.—30. Tangential section. Note small cell size. — 31–32. *Scaevola gaudichaudii (Carlquist 2380)*.—31. Transection. Growth rings are evident.—32. Tangential section. — Scale of magnification shown beside Fig. 1.

Grooves and bands have been suggested as indicators of xeromorphy in Asteraceae (Carlquist, 1966*c*) and other families (Webber, 1936).

Diameter of pits in Goodeniaceae ranges from 3 to 7μ (to 9μ in *S. glabra* because elliptical pits are extremely common). This range is not great, and no correlations are proposed. However, pits in vessels of Australian Goodeniaceae seem generally smaller than those in the insular species of *Scaevola*.

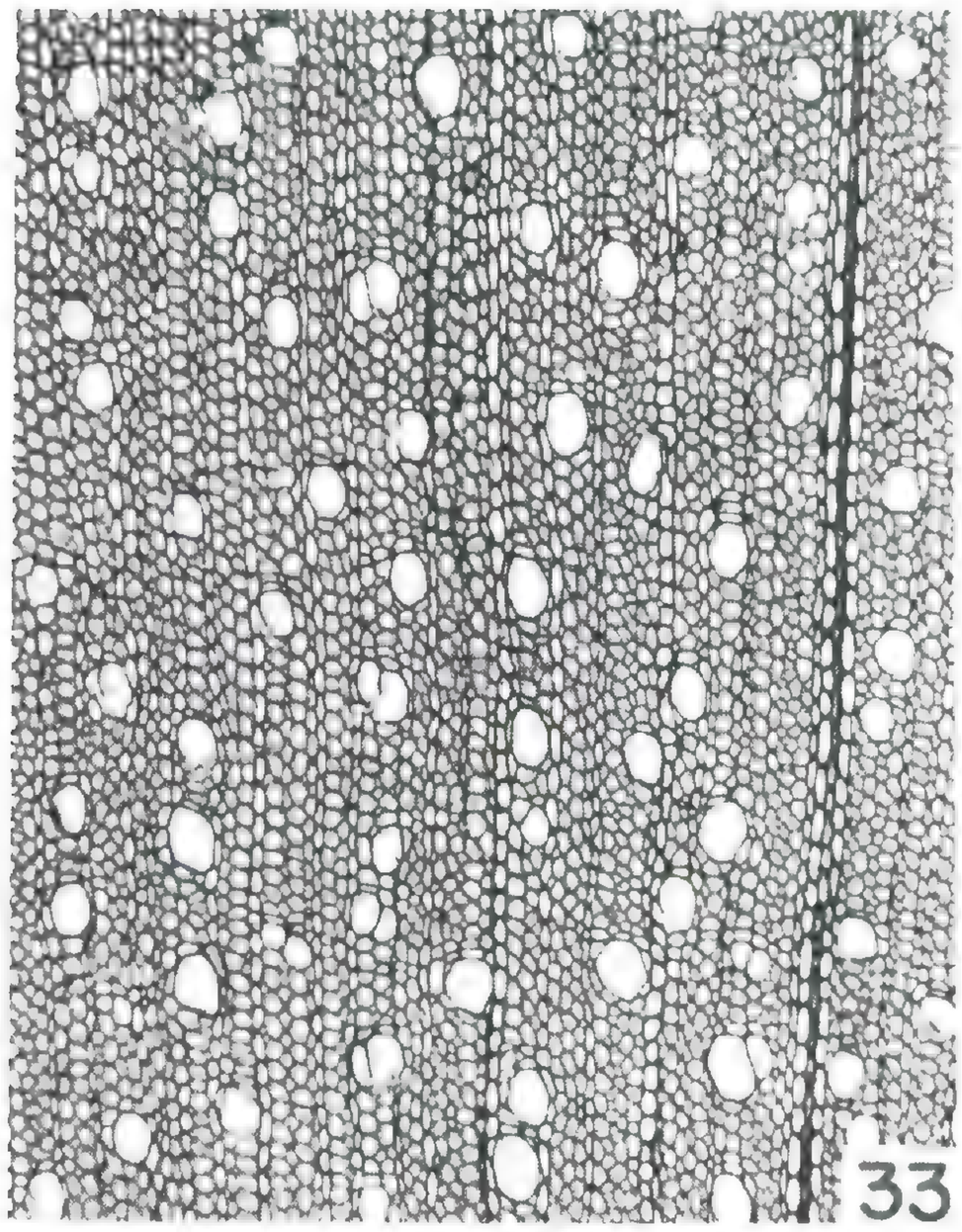
Grouping.—In studies of woods of Astereae (Carlquist, 1960*b*) and other tribes of Asteraceae, degree of vessel grouping proved to be an interesting indicator of xeromorphy or phyletic specialization, or perhaps both. Goodeniaceae as a whole have a much lower degree of vessel grouping than do Astereae as a whole, and this probably reflects lower degree of specialization in woods of Goodeniaceae. The high figure for the family is in *Scaevola beckii,* the distinctive serpentine species of New Caledonia. Other species are low in degree of vessel grouping, and minor differences probably are not significant.

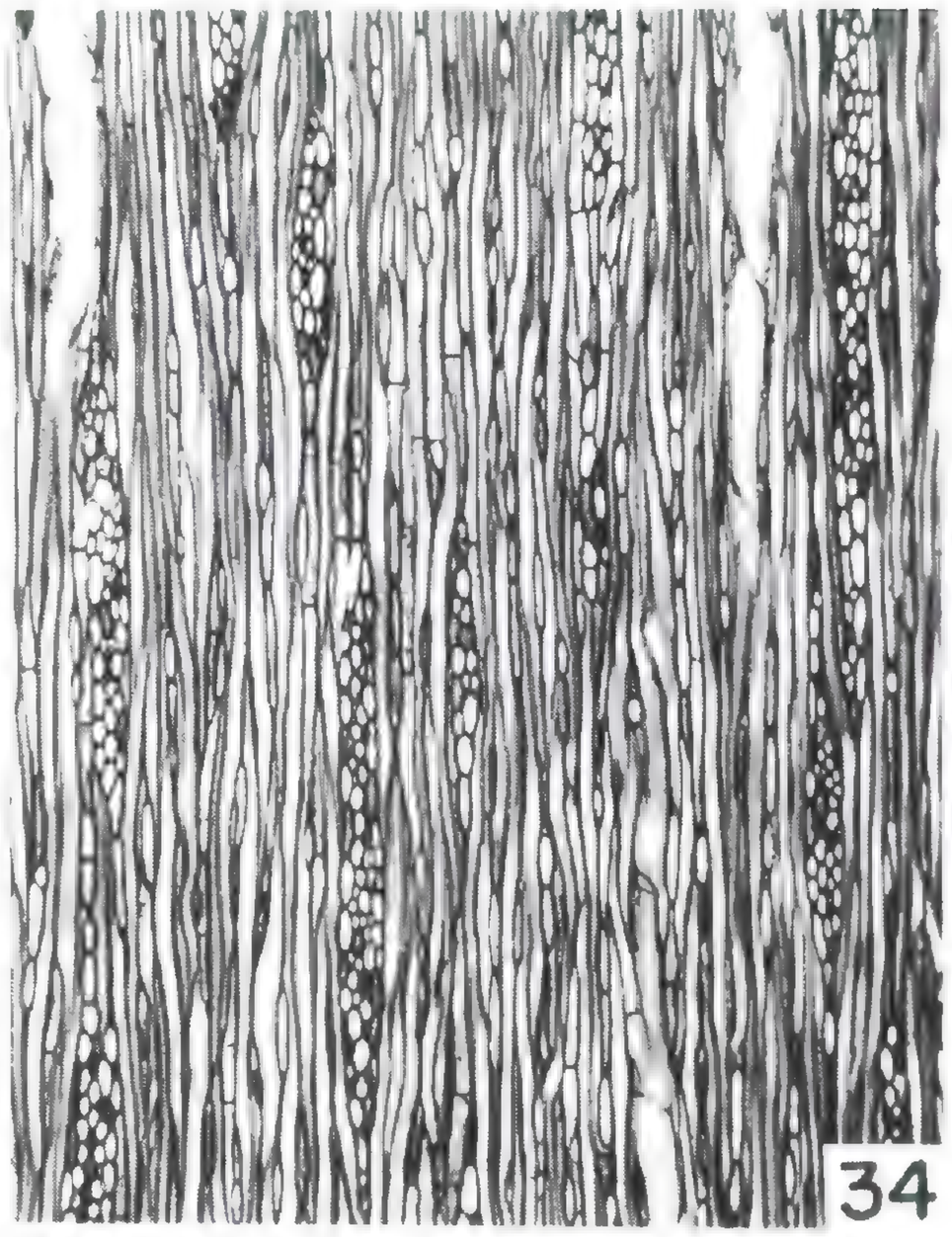
TRACHEIDS AND FIBER-TRACHEIDS

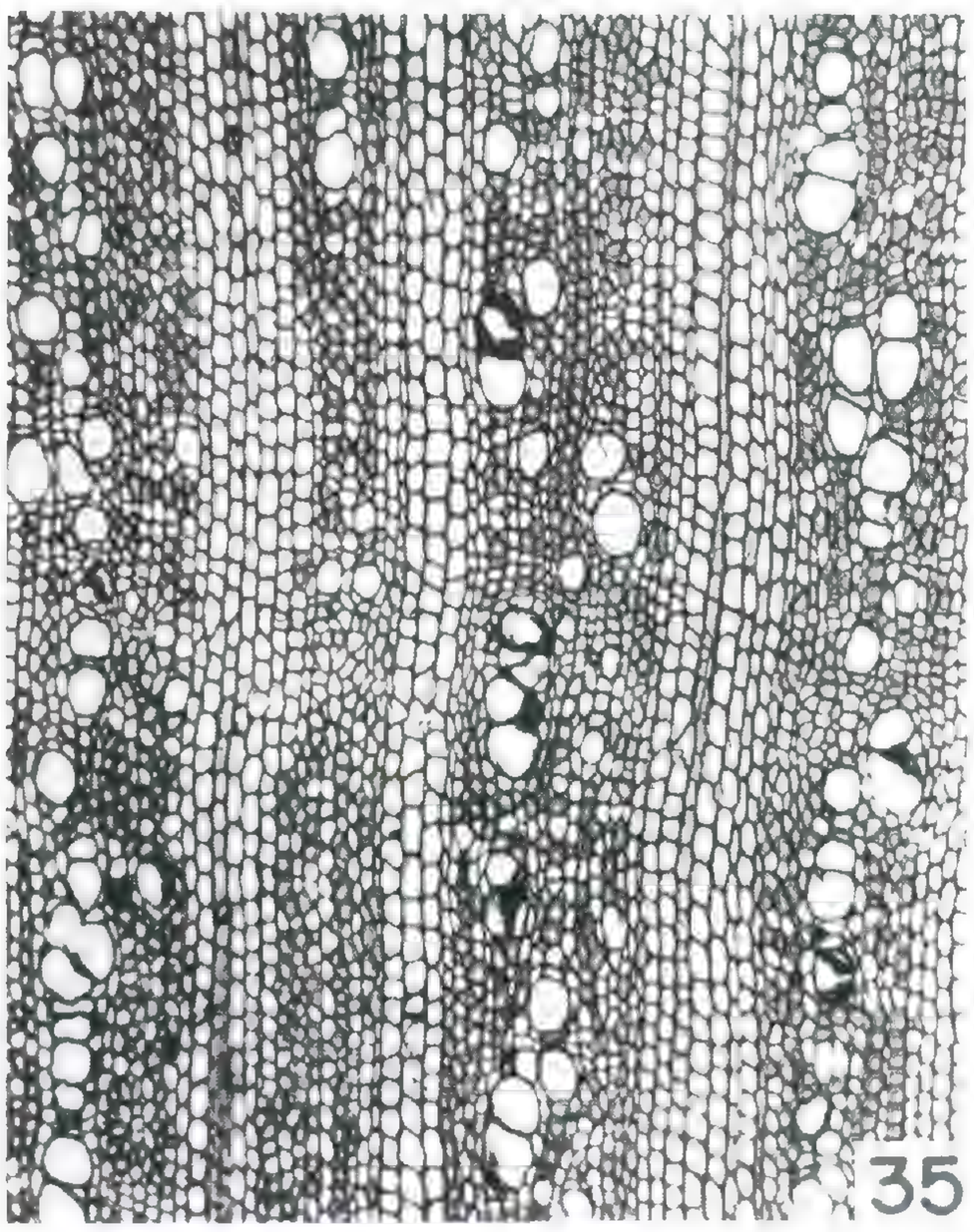
Borders are clearly present on pits of all imperforate tracheary elements in Goodeniaceae, and no libriform fibers can be said to be present. Designating the imperforate elements as tracheids or fiber-tracheids is a rather arbitrary matter. For convenience, I have used a criterion employed elsewhere (Carlquist, 1961). If the ellipse of the pit aperture extends beyond the outline of the pit cavity, the element is designated as a fiber-tracheid; if the aperture is shorter than the diameter of the pit cavity, the element is said to be a tracheid. The distinction in the case of Goodeniaceae is not a very great one, for most elements have pits in which the aperture is only slightly longer than, or slightly shorter than, the diameter of the pit cavity. Consequently, stress should not be placed upon this feature, summarized in the last column of Table 1. However, there seems to be a correlation between increasing woodiness (or arborescence) and the tendency toward production of fiber-tracheids rather than tracheids. The Hawaiian species of *Scaevola* in particular might be cited in this regard.

Fiber-tracheids and tracheids in Goodeniaceae range in wall thickness, but exceptionally thick walls characterize *Scaevola glabra* (Fig. 35, 36), *S. tahitensis* (Fig. 27, 28), *S. beckii* (Fig. 21, 22), and *S. spinescens* (Fig. 15, 16). In *S. spinescens,* fiber-tracheids and tracheids are relatively narrow, so that with thick walls, the lumina of the cells are virtually occluded, a fact noted by Vesque (1876). Tracheids and fiber-tracheids of *S. gaudichaudiana* (Fig. 33), *S. plumieri* (Fig. 37), *S. taccada* (Fig. 39), and *S. oppositifolia* (Fig. 41), look thin-walled, but these cells are relatively wide, so that the wall thickness leaves room for a lumen much wider than that of *S. spinescens.*

Gelatinous walls characterize tracheids, fiber-tracheids, and vessel elements of many Goodeniaceae, judging from staining reactions and shrinkage patterns within walls. These were seen most strikingly in *Scaevola glabra, S. platyphylla,* and *S. spinescens.*







FIGURES 33–36.—Wood sections of upland Hawaiian species of *Scaevola*. — 33–34. *Scaevola gaudichaudiana* (USw-15333).—33. Transection. Vessels are rather wide and isolated.—34. Tangential section. Multiseriate rays are rather short and narrow. — 35–36. *Scaevola glabra* (*Carlquist 1975*).—35. Transection. Note deposits in vessels; axial parenchyma is abundant.—36. Tangential section. Rays are very wide and high; vessel elements are rather long. — Scale of magnification shown beside Fig. 1.

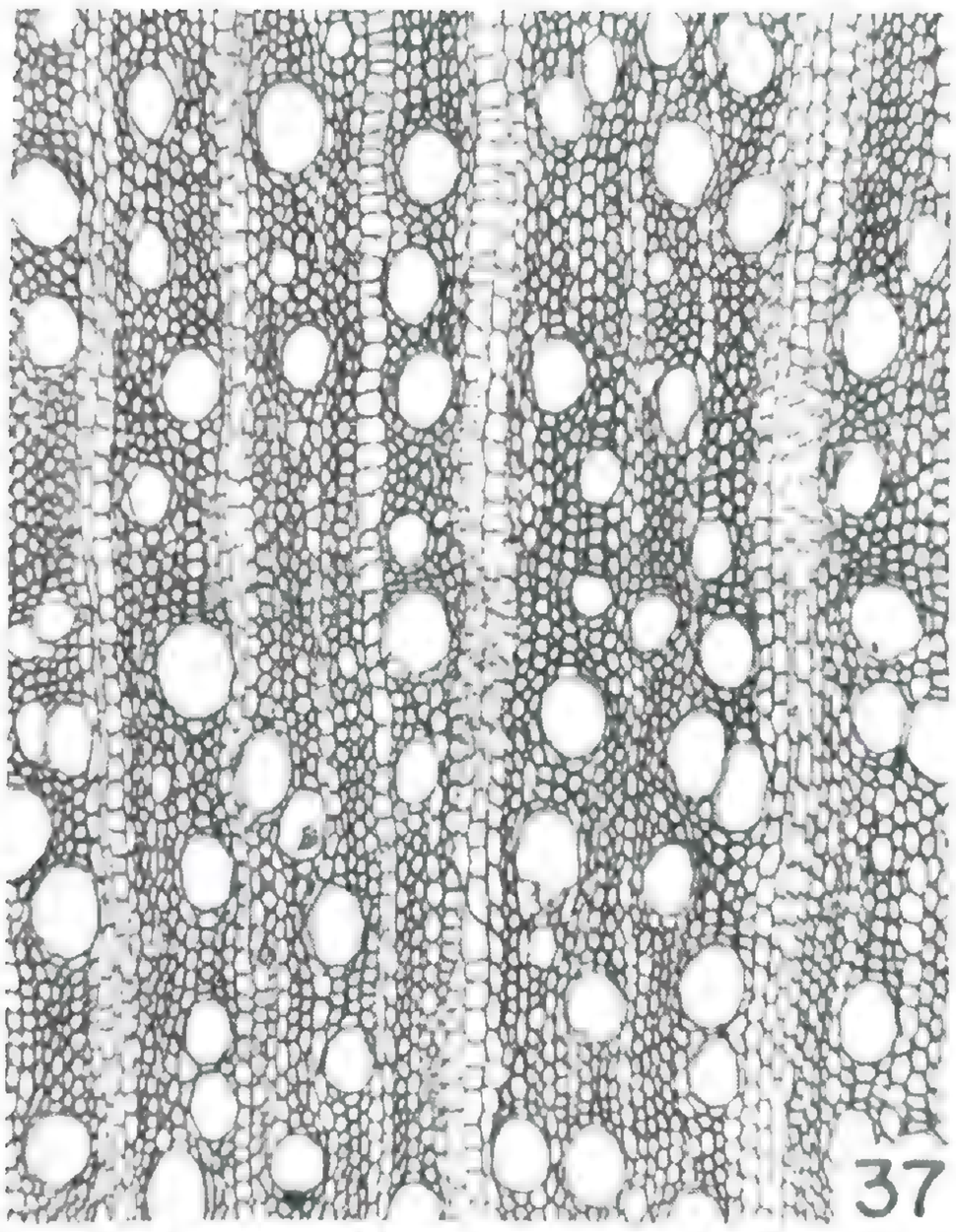
VASCULAR RAYS

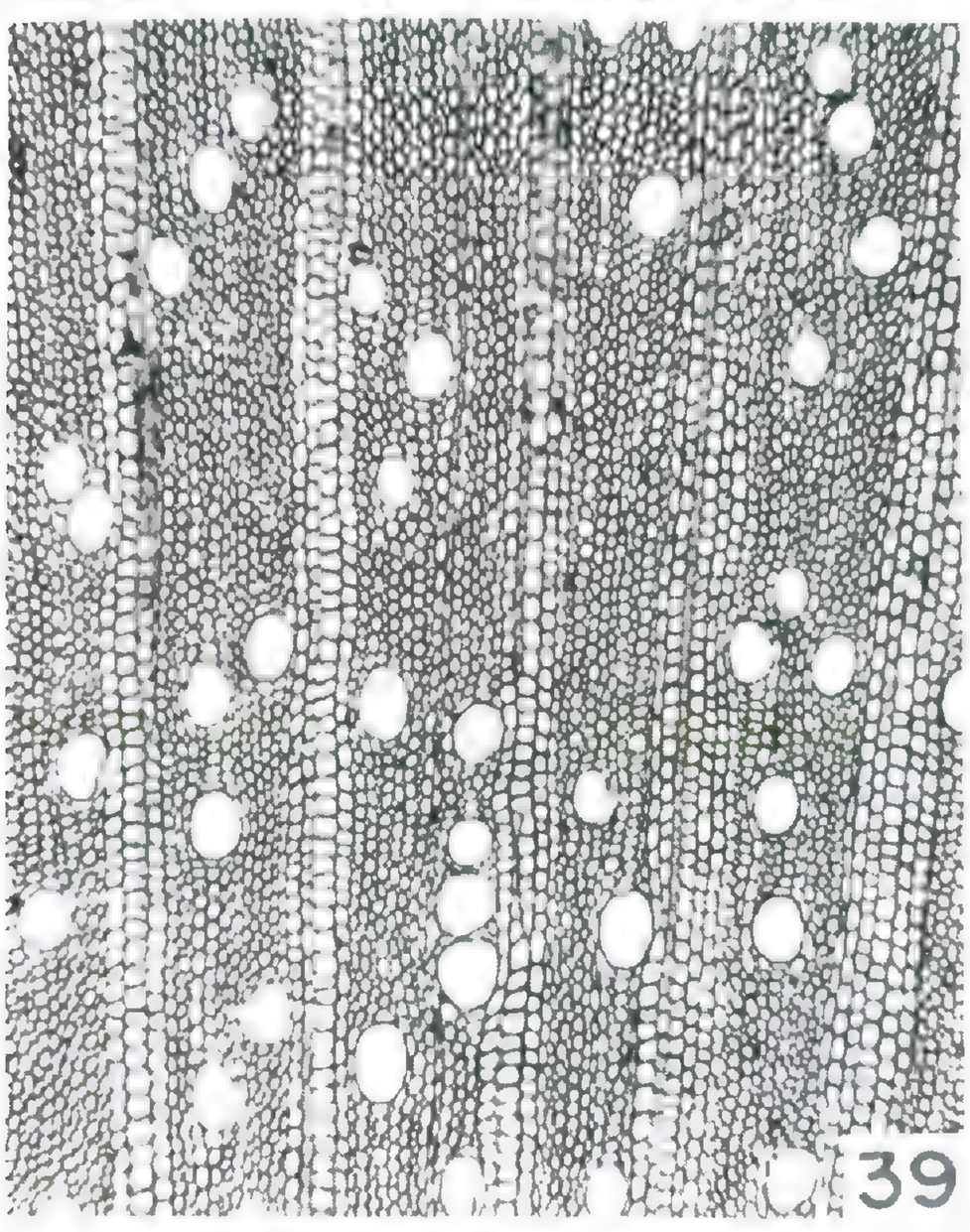
Dimensions.—Species with exceptionally tall rays (averaging more than 3 mm) for Goodeniaceae include *Scaevola chamissoniana* var. *cylindrocarpa, S. glabra* (Fig. 36), *S. oppositifolia, S. paludosa, S. platyphylla, S. porocarya,* and *S. taccada* (Fig. 40). However, rays of Goodeniaceae generally are unusually tall. For example, the average ray height in Asteraceae at large is only 1.44 mm. However, tall rays characterize dicotyledons of various types, and ray height shows no clear correlation with habit. The correlation between ray height and vessel-element length is not perfect in Goodeniaceae, although it is more often true than not. *Scaevola paludosa* has tall rays, but short vessel elements. Short rays occur in the following Goodeniaceae: *Coopernookia strophiolata* (Fig. 4), *Goodenia decurrens* (Fig. 8), *Leschenaultia biloba* (Fig. 12), *Scaevola crassifolia, S. dielsii, S. "procera," S. sericophylla,* and *Verreauxia reinwardtii.* These species all have relatively short vessel elements, although again the correlation of short rays with short vessel elements is imperfect.

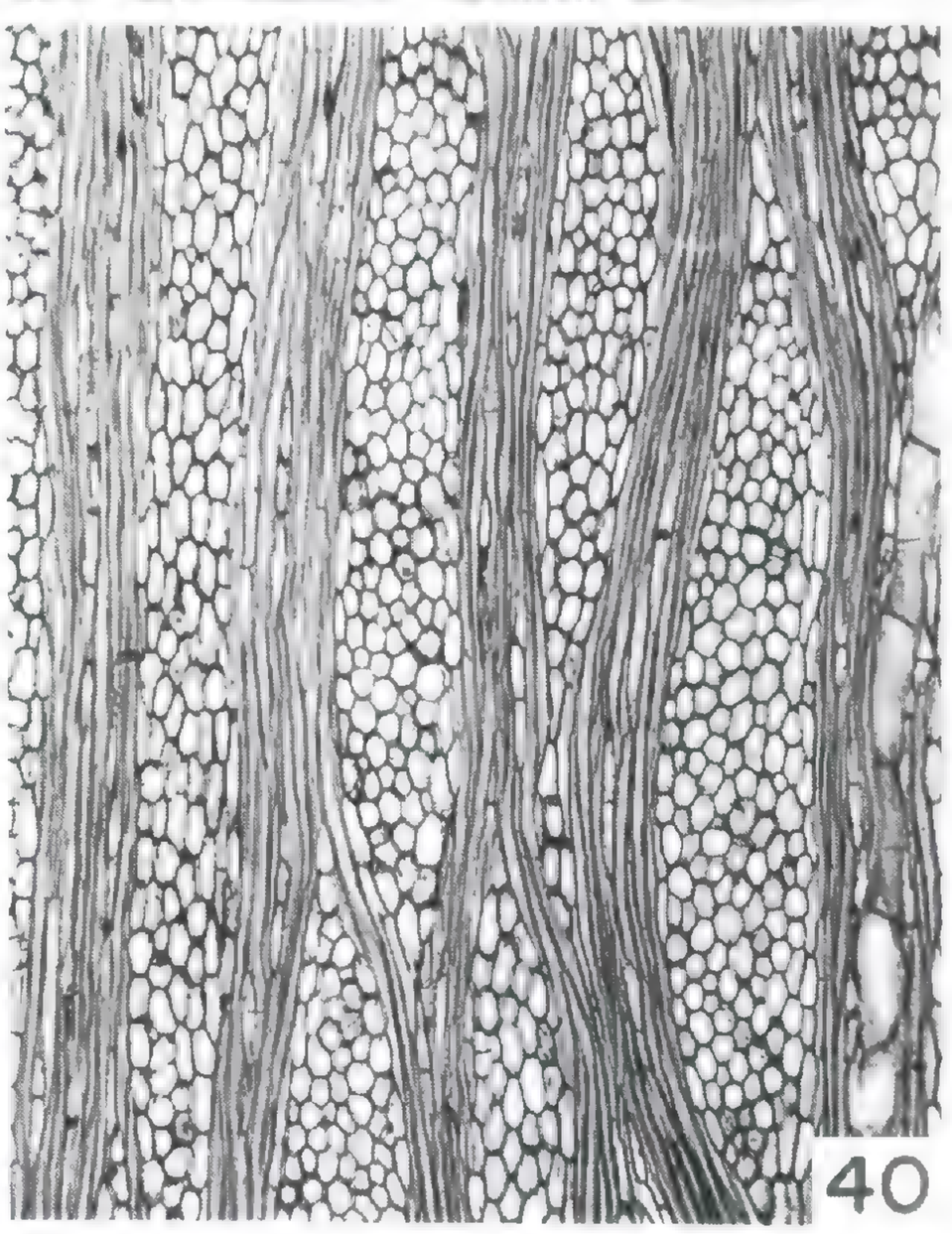
Cell Shape.—With respect to ray histology, Goodeniaceae show some interesting tendencies. Predominance of erect ray cells, a criterion cited earlier (Carlquist, 1962) as an indication of paedomorphosis, characterizes many Goodeniaceae: *Dampiera brownii, Goodenia decurrens, G. ovata, G. scapigera, Leschenaultia biloba, Scaevola coriacea, S. floribunda, S. glabra, S. indigofera, S. montana, S. nitida, S. platyphylla, S. plumieri, S. sericophylla, S. taccada,* and *S. tahitensis.* There is a correlation between erectness of ray cells and longer vessel elements. Both may be related to mesomorphy, as seems the case in Asteraceae (Carlquist, 1966*c*). Predominance of procumbent cells characterizes only a few Goodeniaceae: *Coopernookia polygalacea, C. strophiolata, Scaevola holosericea, S. kilaueae, S. porocarya, S. spinescens,* and *S. tomentosa.* All but one of these is from a rather dry habitat in Australia; *S. kilaueae* is a species of an area which is effectively dry (new lava of Kilauea) in the Hawaiian Islands.

Rayless woods are, in effect, those in which ray cells are exclusively erect, and thus equivalent to libriform fibers (or axial parenchyma). Raylessness characterizes all of the species of *Leschenaultia.* At an early stage, *Leschenaultia* woods are definitely rayless, as shown for *L. splendens* (Fig. 9–10). Later in ontogeny, rays developed, as shown for *L. biloba.* The same is true of *Goodenia ovata* (Fig. 5–6). This relation between ontogeny and raylessness was noted by Barghoorn (1941).

Rayless woods tend to occur in herbaceous groups which show juvenilism (Carlquist, 1962). In particular, herbaceous groups which show a limited increase in woodiness tend to include rayless species. This appears to be true in Goodeniaceae. *Goodenia ovata* suggests this clearly, for the secondary xylem originates not from the vascular bundles of the primary cylinder, but outside them (Fig. 5) as mentioned and illustrated by both Vesque (1876) and Krause (1912). This condition can be said to represent an anomalous secondary xylem condition and possibly a return to woodiness in a phylad that has lost the ability to form secondary xylem in bundles of the primary cylinder. If so, the relationship between herbaceous groups and raylessness would certainly be clear.







FIGURES 37–40.—Wood sections of littoral species of *Scaevola*. — 37, 38. *Scaevola plumieri* (*W. G. Earle s.n.*).—37. Transection. Note wide vessels. —38. Tangential section. Vessel elements are relatively long. — 39, 40. *Scaevola taccada* (*Carlquist 701*). —39. Transection. Vessels are relatively sparse and isolated.—40. Tangential section. Rays are wide and tall. — Scale of magnification shown beside Fig. 1.

Ray Cell Walls.—Relatively thin-walled ray cells characterize most Goodeniaceae. These cells are lignified in nearly all species. A few cells of larger rays in *Goodenia decurrens* (Fig. 8) are not lignified and tend to collapse. Notably thick ray cell walls were observed in *Scaevola beckii* (Fig. 22), *S. dielsii, S. glabra* (Fig. 36), *S. plumieri* (Fig. 38), and *S. spinescens* (Fig. 16). Conspicuous pits characterize ray cells of *Coopernookia polygalaceae* (Fig. 46) and *Dampiera brownii.* Notably large ray cells occur in *Scaevola glabra* (Fig. 36), *S. plumieri* (Fig. 38), and *S. taccada* (Fig. 40).

Uniseriate Rays.—Uniseriate rays are present in all Goodeniaceae studied (except the rayless stems of *Leschenaultia*). Uniseriate rays are usually composed of erect ray cells. On superficial examination of wood, a uniseriate ray can be confused with axial parenchyma strands. The latter occur as shorter series, roughly the length of vessel elements, that form smooth fusiform outlines as seen in a tangential section. The cells of a uniseriate ray are more rounded and undulate in outline, and ordinarily they are taller than a strand of axial parenchyma.

AXIAL PARENCHYMA

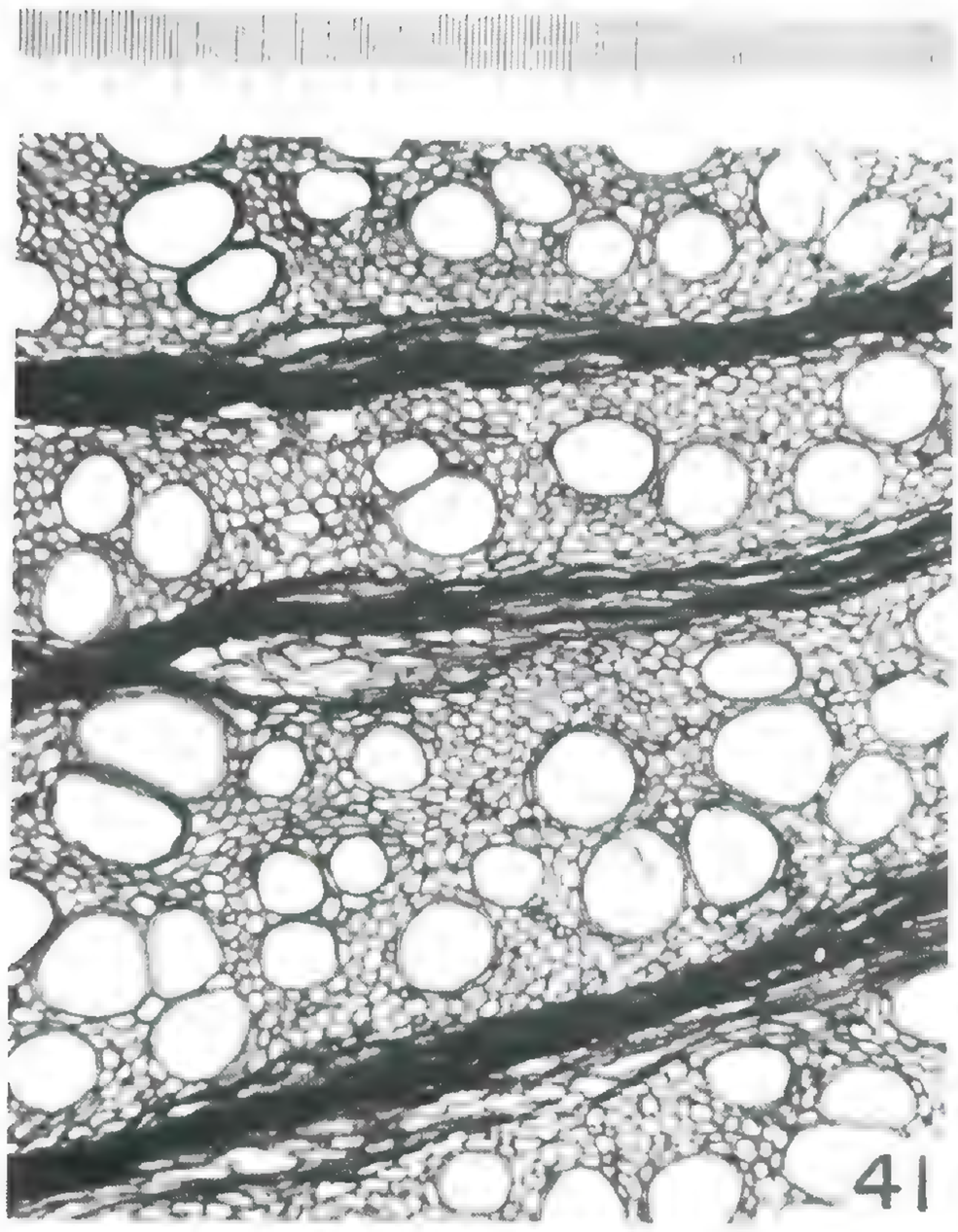
The range in axial parenchyma in Goodeniaceae is rather marked, as can be seen in Table 1. Axial parenchyma is absent or nearly so in *Leschenaultia.* Axial parenchyma is absent except for a very few cells at the end of a growth ring in *Coopernookia polygalacea, C. strophiolata, Dampiera brownii, Goodenia decurrens, Scaevola dielsii, S. fasciculata, S. paludosa, S. platyphylla,* and *S. sericophylla.* Interestingly, these are all relatively short-lived perennials from Australia. Consistent formation of parenchyma seems characteristic of longer-lived species in Goodeniaceae.

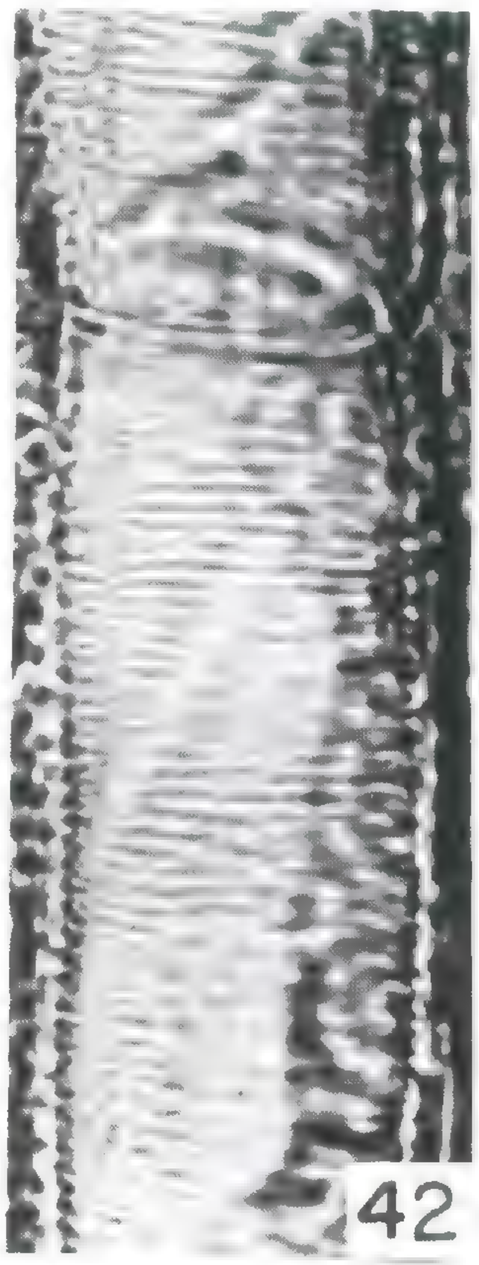
Very sparse axial parenchyma arranged in a diffuse fashion characterizes most species of Goodeniaceae. Where a sparse axial parenchyma in a diffuse distribution occurs, one cannot really distinguish between apotracheal and paratracheal (vasicentric) satisfactorily, because a few cells will be adjacent to vessels although many will not be. In a few Goodeniaceae, however, only vasicentric axial parenchyma cells were seen: *Scaevola beckii, S. plumieri,* and *S. taccada.* This would seem an interesting species character, for it emphasizes the difference between these three species and the purple-fruited montane insular species of *Scaevola,* which have either abundant or sparse diffuse parenchyma.

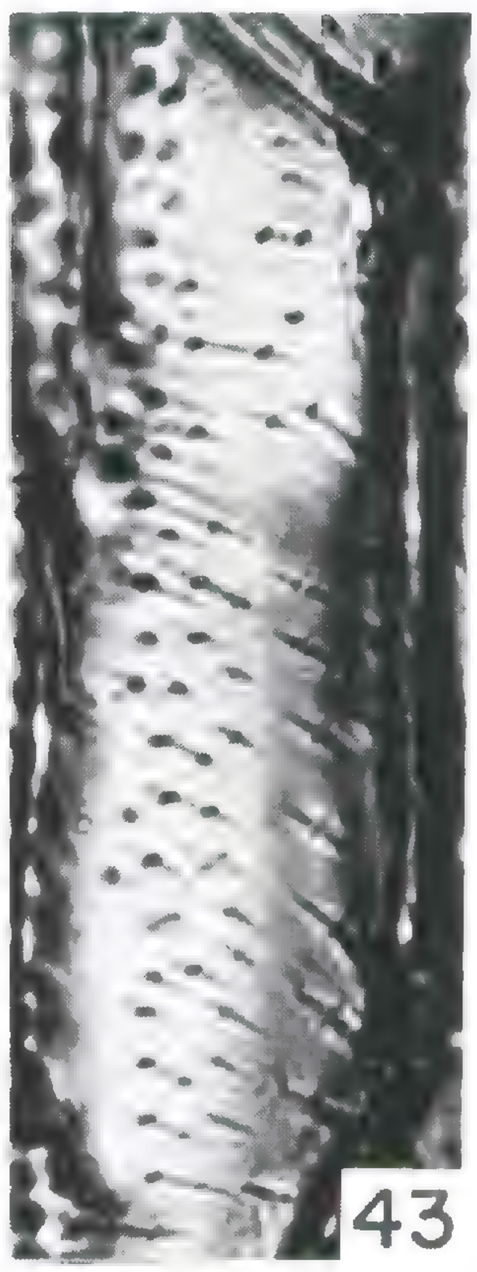
Relatively abundant diffuse parenchyma characterizes a few Goodeniaceae: *Goodenia ovata, Scaevola coriacea, S. crassifolia, S. floribunda, S. glabra, S. montana, S. oppositifolia, S. spinescens,* and one collection of *S. taccada.* These are all woody rain forest plants or succulent plants. Correlation with mesomorphy is suggested by the fact that abundance of axial parenchyma is greatest in the species adapted to the wettest forest: *S. glabra* of the Hawaiian Islands.

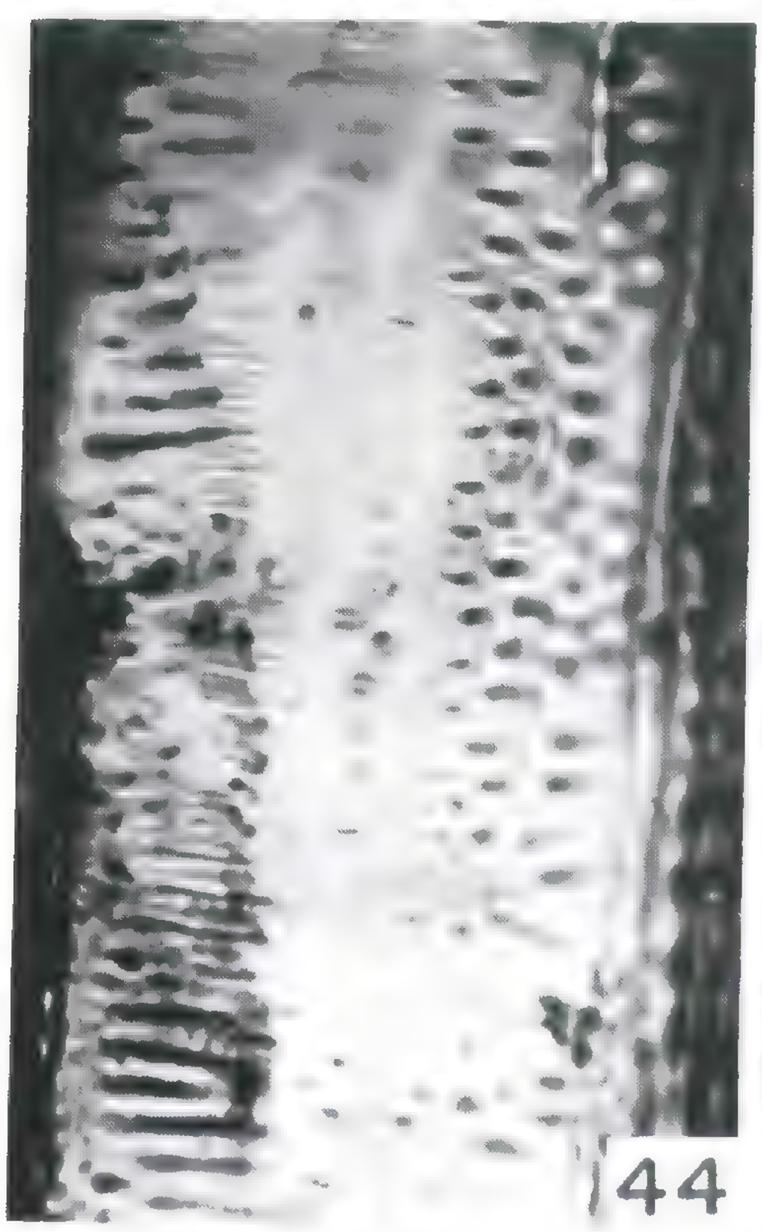
GROWTH RINGS

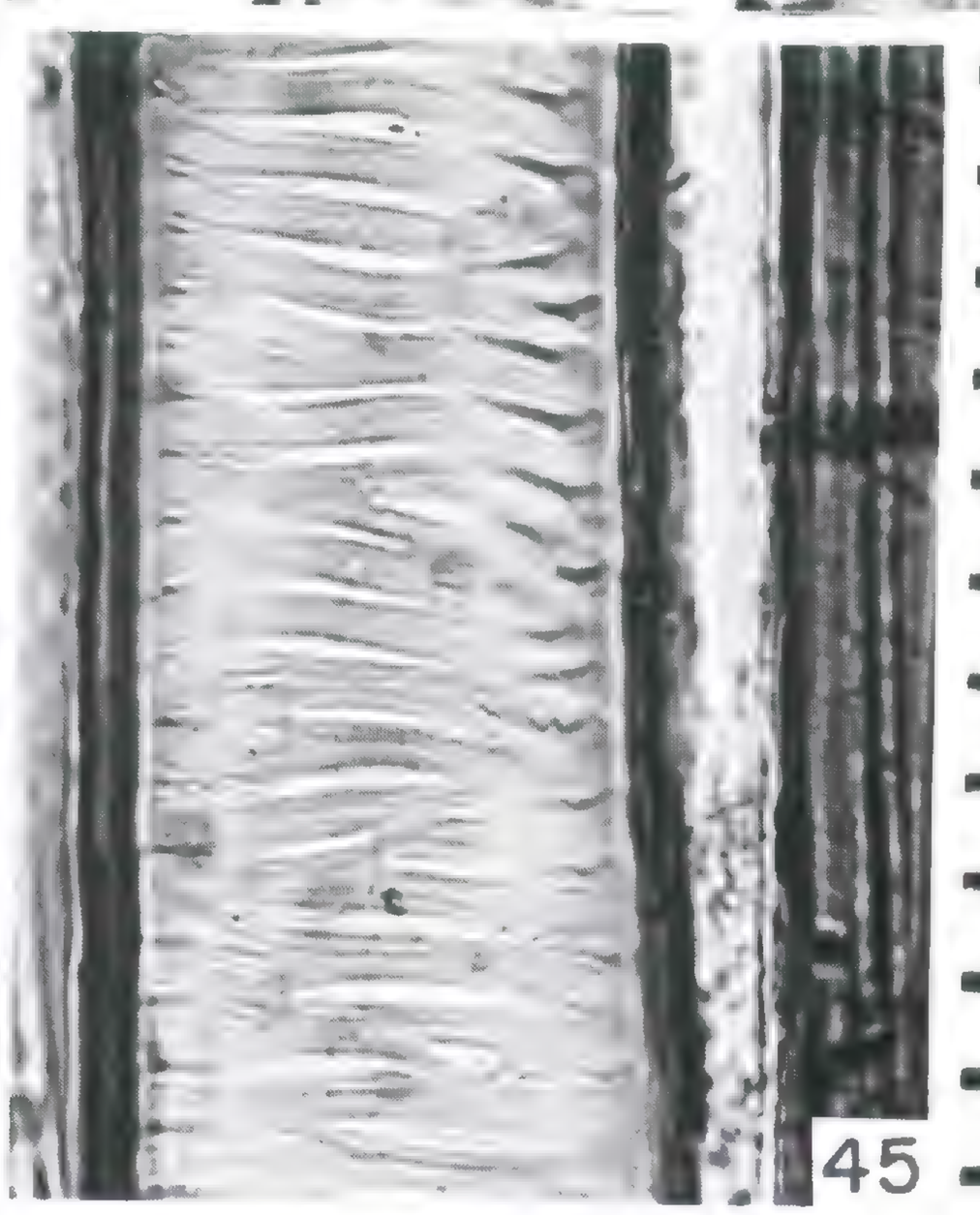
Growth rings are present in many Goodeniaceae, particularly those of temperate Australia, but few are strongly pronounced. Probably none could be called truly ring-porous. Growth rings have been illustrated here for *Coopernookia poly-*











FIGURES 41–45. — 41. *Scaevola oppositifolia (Carlquist 1386)*. Transection. The wide vessels correspond to the scandent habit of this species.—Scale of magnification shown above. 42 45. Portions of vessel walls to show types of lateral-wall pitting.—42. *Coopernookia polygalacea (Carlquist 3475)*. Fine bands are evident.—43. *Scaevola spinescens (Carlquist 914)*. Grooves interconnect pits adjacent in a helix. 44. *Scaevola chamissoniana* var. *chamissoniana (Carlquist 2241)*. Scalariform pitting at left, alternate pitting at right in this vessel.—45. *Scaevola glabra (Carlquist 1975)*. While some vessels show a near-perfect scalariform pattern, this vessel shows a transitional or near-scalariform pattern.—Scale of magnification for Fig. 42–45 is shown to right of Fig. 45. Divisions 10μ each.

galacea (Fig. 1, top), *C. strophiolata* (Fig. 3), *Goodenia decurrens* (Fig. 7, middle), *Leschenaultia biloba* (Fig. 11, top), *Scaevola spinescens* (Fig. 15), *S. fasciculata* (Fig. 17), *S. tahitensis* (Fig. 27), and *S. gaudichaudii* (Fig. 31). Rain forest species such as *Scaevola glabra* (Fig. 35) show very subtle or virtually no growth ring phenomena, whereas the most marked growth rings are seen in the shrubby perennials of southwestern Australia.

INSOLUBLE DEPOSITS

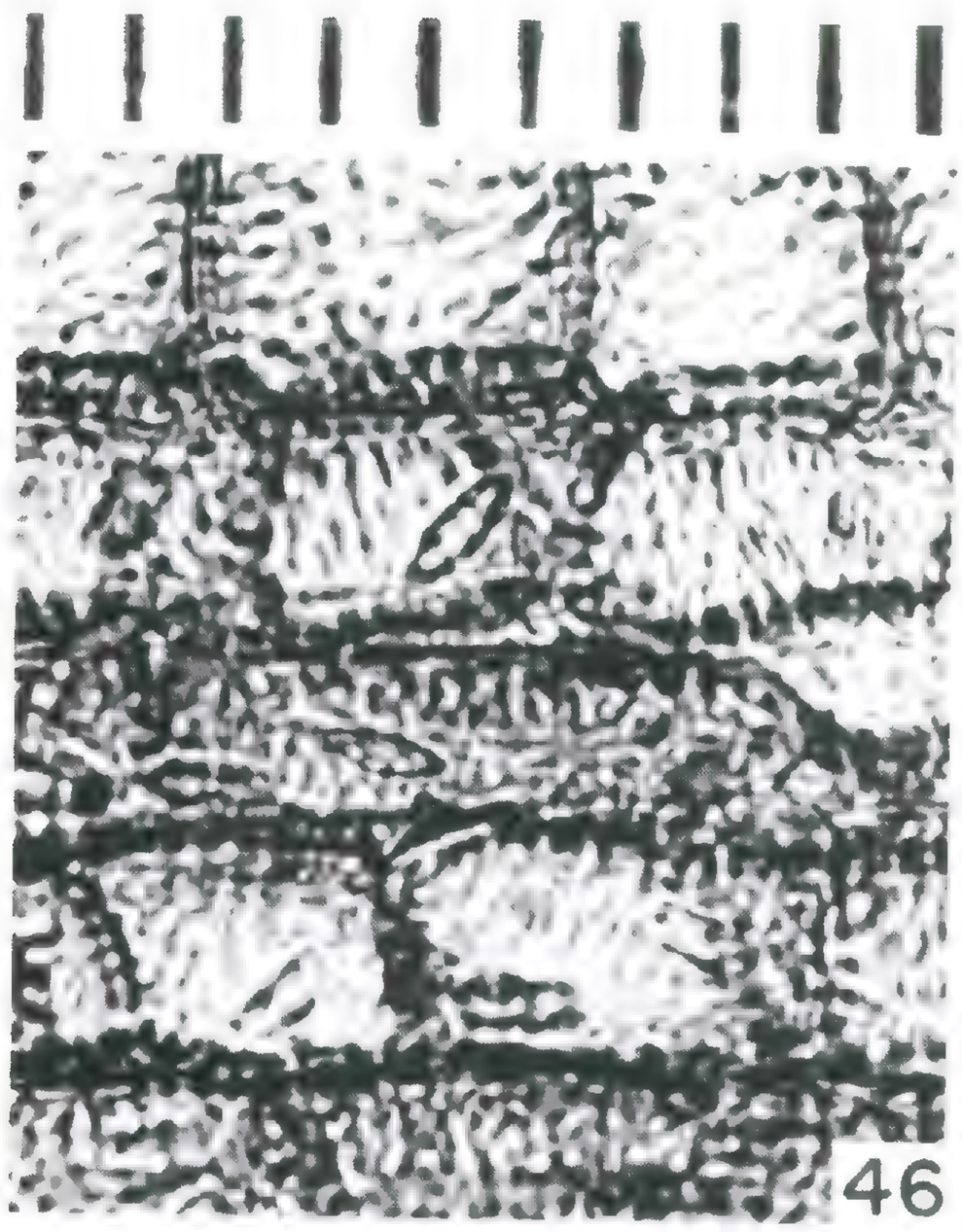
Deposits insoluble in water, alcohol, and xylene are present in woods of many Goodeniaceae. These appear resin-like, but even that vague term might be misleading. Chemical identification of these prominent deposits is very much needed.

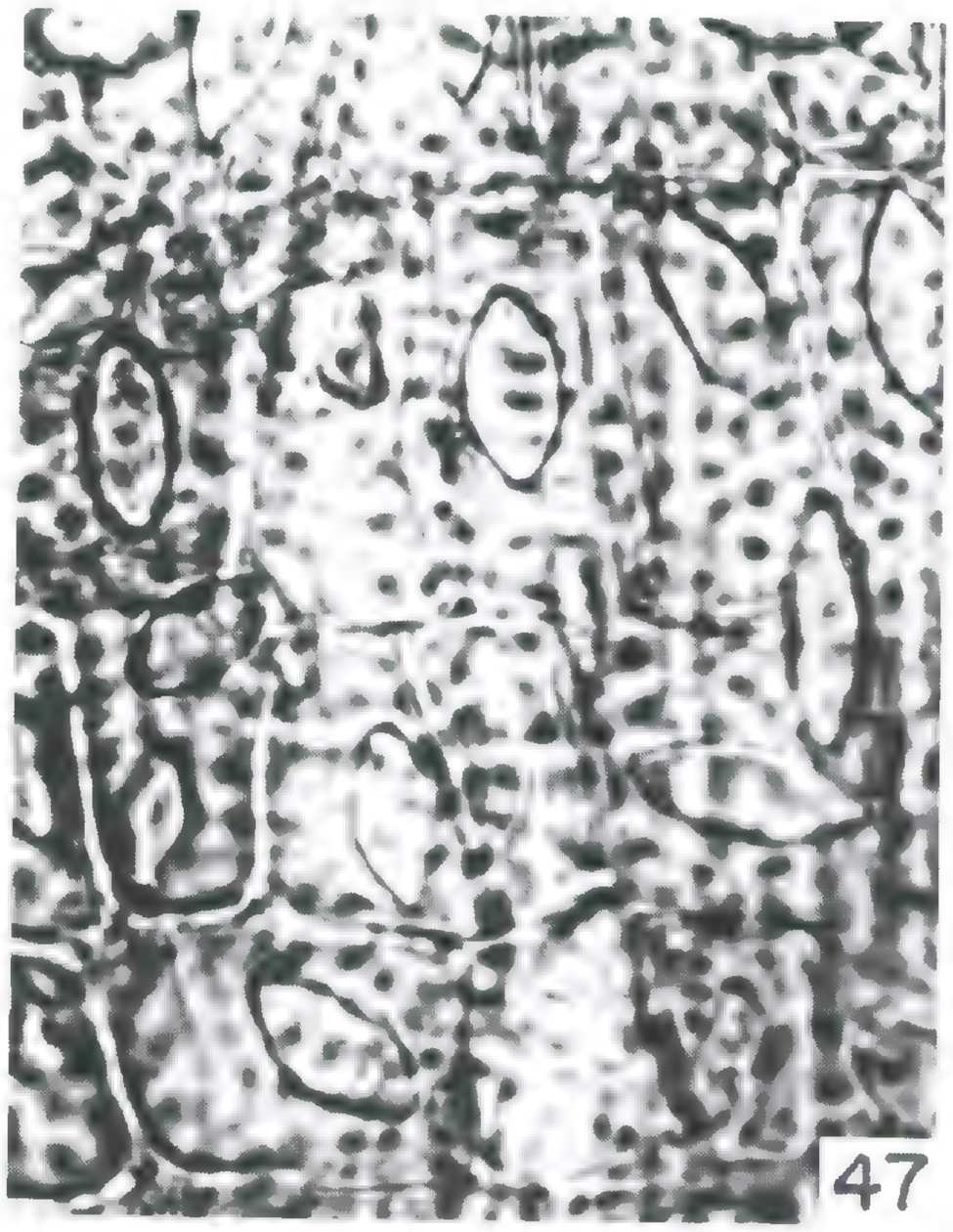
Massive accumulations of these materials in vessels, together with droplets in parenchyma cells, were observed in the following species: *Dampiera brownii* (Fig. 13), *Goodenia scapigera, Leschenaultia splendens* (a few vessels near pith, Fig. 9), *Scaevola beckii* (Fig. 21–22), *S. chamissoniana* var. *bracteosa, S. coriacea* (Fig. 29–30), *S. crassifolia, S. gaudichaudiana* (Fig. 33–34), *S. gaudichaudii* (Fig. 31), *S. glabra* (Fig. 35–36), *S. holosericea, S. indigofera, S. kilaueae, S. oppositifolia* (Fig. 41), *S. spinescens* (Fig. 15–16), and *S. tahitensis* (Fig. 27–28). Scantier accumulations of these materials, present only as droplets in parenchyma and other cells, were observed in woods of *Coopernookia polygalacea* (Fig. 1–2), *Goodenia decurrens* (Fig. 7–8), *Scaevola fasciculata* (Fig. 17–18), *S. mollis, S. montana* (Fig. 23), *S. "procera,"* and *S. taccada* (Fig. 39–40). Goodeniaceae in which few or no deposits were observed in woods include *Coopernookia strophiolata* (Fig. 3–4), *Dampiera glabrescens, Goodenia ovata* (Fig. 5–6), *Leschenaultia biloba* (Fig. 11–12), *Scaevola dielsii, S. floribunda* (Fig. 25–26), *S. nitida* (Fig. 19–20), *S. paludosa, S. platyphylla, S. plumieri* (Fig. 37–38), *S. porocarya, S. sericophylla, S. tomentosa,* and *Verreauxia reinwardtii.*

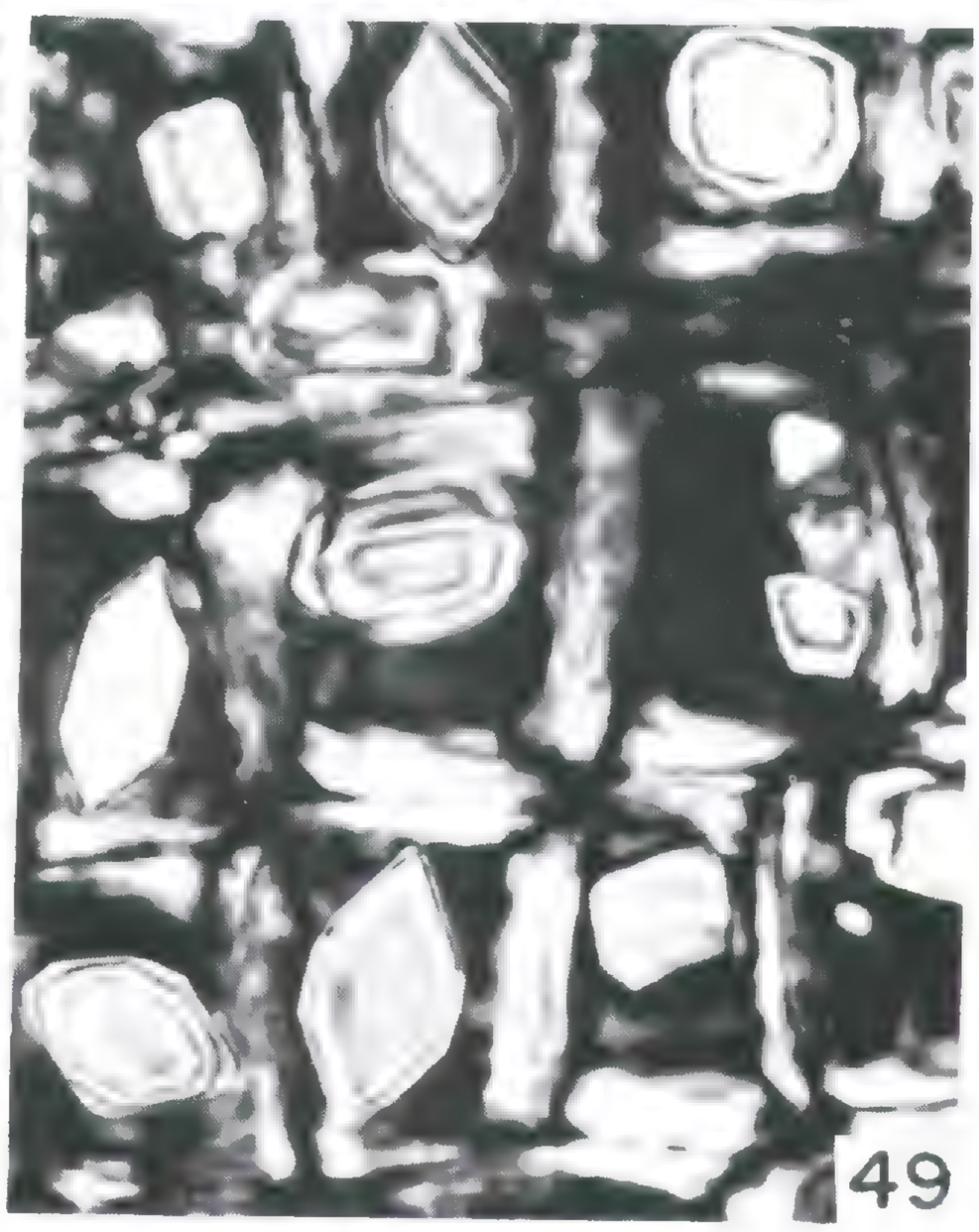
CRYSTALS

Crystals, presumably composed of calcium oxalate, occur in ray cells of many Goodeniaceae, as shown in Table 1 and Fig. 46–49. These crystals show birefringence in polarized light, often exhibiting irridescent colorations (Fig. 49). Crystals of Goodeniaceae could all be described as rhombic. A few are 4-sided rhombic as seen in face view; in the majority, additional faces are added, so that a hexagonal appearance is achieved (Fig. 49). In a few, the ends develop flattened faces so that an octagonal shape occurs.

Large hexagonal crystals are abundant in rays of the following species: *Coopernookia strophiolata* (Fig. 47), *Scaevola crassifolia, S. dielsii, S. holosericea, S. nitida, S. oppositifolia, S. porocarya* (Fig. 48), *S. sericophylla, S. spinescens* (Fig.49), and *S. tomentosa.* Somewhat smaller crystals, more elongate in shape, were observed in *Coopernookia polygalacea* (Fig. 46), *Scaevola coriacea, S. gaudichaudii, S. kilaueae, S. paludosa,* and *S. platyphylla. Scaevola beckii* has distinctive crystals: octagonal in face view, with a rather rounded outline, and pronounced fractures and gaps in the central portions.







FIGURES 46–49.—Portions of rays from radial sections of wood of Goodeniaceae showing crystals. — 46. *Coopernookia polygalacea* (*Carlquist 3475*). Crystals are small and somewhat obscured by prominent pitting in ray cells. — 47. *Coopernookia strophiolata* (*Carlquist 3393*). Crystals are medium to large and mostly hexagonal in face view. — 48. *Scaevola porocarya* (*Carlquist 2957*). Crystals are medium-sized and hexagonal (rectangular as seen in side view). — 49. *Scaevola spinescens* (*Carlquist 914*). Crystals photographed with polarized light; these would be relatively large in Goodeniaceae as a whole. — Scale of magnification for Fig. 46–49 is shown above Fig. 46. Divisions 10μ each.

There appears to be a very clear correlation between xeromorphy and presence of crystals. None of the upland montane scaevolas of Pacific islands have crystals. The only exception is *S. oppositifolia,* which does not belong to sect. *Scaevola* in any case.

In addition to rhombic crystals in rays, druses occur in pith and cortex of Goodeniaceae (Colozza, 1908; Krause, 1912; Metcalfe & Chalk, 1950). In the present study, such druses were observed in pith of *Scaevola taccada* and *S. tahitensis.* They probably occur in more species, but pith and cortex were not investigated.

Discussion and Conclusions

Systematic application of data from wood anatomy in Goodeniaceae is obvious enough. Contrasts and similarities are self-evident in the table, illustrations, and text of this paper. However, as the reader will have noticed, adapation of Goodeniaceae to diverse habitats has carried with it marked shifts in modes of anatomical structure. These modes may be summarized as follows:

Australian Short-Lived Perennials and Short-Lived Shrubs.—This group includes *Coopernookia, Goodenia, Dampiera,* some species of *Scaevola.* It possesses relatively short, narrow vessels, which are numerous per area of transection. Perforation plates are almost invariably simple; lateral-wall pits are relatively small and alternate. Grooves along vessel walls or even bands *(Coopernookia)* may be present. Tracheids and fiber-tracheids are present. Rays of some species contain a preponderance of procumbent cells, while others (*Leschenaultia* spp.; *Goodenia ovata*) show preponderance of erect ray cells and even raylessness earlier in the ontogeny of stems. Some wide, short rays are present *(Goodenia decurrens* and *Scaevola spinescens),* but most species in this group have relatively narrow rays of medium height. Axial parenchyma is absent or very sparse and is sometimes present only as a few cells in growth rings. In no species is it abundant. Growth rings are prominent, and most species have large rhomboidal crystals in the rays.

Goodenia ovata is an exception to the above pattern, but it occupies a mesic locality, so that its relatively long, wide vessels, relatively abundant axial parenchyma, lack of growth rings, and lack of crystals—all of these characteristics of the group below—are understandable. *Scaevola oppositifolia* is also exceptional in virtually the same respects (except that it has crystals), and again, it occupies mesic sites in Queensland and the Indo-Malaysian islands.

Montane Pacific Species of Scaevola.—These species are characterized by long, relatively wide vessel elements, which are rather few per unit area of transection. There is a strong tendency toward transitional or even scalariform lateral-wall pitting on vessels; grooves or bands are absent. Perforation plates are basically simple, but occasional scalariform plates (often with aberrant bars) are present. Both tracheids and fiber-tracheids are present, but there is a tendency toward the latter. Corresponding to greater length of vessel elements, erect ray cells are relatively more common than procumbent cells. Rays are mostly relatively tall, of varying width (some very wide). Axial parenchyma is diffuse, ranging from sparse to very abundant. Growth rings are few and inconspicuous. Crystals are lacking.

Exceptions to the above pattern are found in lowland insular species which represent less or no adaptation to wet-forest conditions. Thus vessels are narrow in *S. beckii* and *S. gaudichaudii,* short in *S. beckii, S. coriacea, S. gaudichaudii,* and *S. kilaueae.* Procumbent ray cells predominate in *S. kilaueae.* Crystals are present in rays of *S. beckii, S. coriacea, S. gaudichaudii,* and *S. kilaueae.* In these respects, *S. beckii, S. coriacea, S. gaudichaudii,* and *S. kilaueae* show greater xeromorphy and more resemblance to the Australian Goodeniaceae.

Maritime Scaevolas.—Surprisingly, the maritime scaevolas resemble the wet-forest species much more than they do the Australian species. Growth in areas of high salinity is not accompanied by xeromorphy. Evidently the succulent nature of these species has as a consequence a mesomorphic pattern, instead. This appears also to be true in species of *Euphorbia* (Carlquist, 1970 *b*), a group which, like *Scaevola,* is basically herbaceous and has adapted to a wide range of habitats. The parallels between wood anatomy in *Euphorbia* and that of *Scaevola* are quite marked, in fact.

Increased arborescence and adaptation to mesic, relatively uniform conditions by an herbaceous group are well shown by montane insular species of *Scaevola.* These features, detailed above, are placed in relief by the contrasting patterns of the lowland insular species of *Scaevola* and the Australian Goodeniaceae. While each group of dicotyledons will show somewhat different tendencies in evolution toward wet forest areas on islands (and continents), all those that clearly seem to follow this course and have been studied in this regard seem to show phenomena referable to paedomorphosis: Asteraceae, Lobelioideae, *Euphorbia.* The fact that juvenilism (or neoteny) is a mechanism that permits change in mature wood patterns seems clear by now. Woods of Goodeniaceae showing these tendencies have been described as having a primitive aspect (Stern & Brizicky, 1958). The explanation for this appearance seems to involve paedomorphosis rather than the simple retention of primitive features. Because primary xylem is a reservoir of relatively primitive features, woods in which primary xylem patterns are protracted will tend to show a more primitive aspect than expected.

However, Goodeniaceae do seem to show some retained primitive features regardless of juvenilism. These include occurrence of tracheids and fiber-tracheids rather than libriform fibers. Libriform fibers are the imperforate tracheary cell type in many other families which are specialized (with respect to gross morphology) as Goodeniaceae: Solanaceae, Campanulaceae, and Asteraceae, for example. The relative abundance of uniseriate rays also seems validly a primitive feature—again, Asteraceae, Solanaceae, and Campanulaceae have a paucity of uniseriate rays. The low degree of grouping in vessels of Goodeniaceae might also be a primitive feature.

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THE CALIFORNIA ISLANDS[1]

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ABSTRACT

The California Islands off the Pacific coast of southern and Baja California display almost diagrammatically the insular phenomena that characterize fringing archipelagos. To a lesser extent they also illustrate some of the insular features associated with oceanic islands. Several of these islands have been much studied and are relatively accessible.

The location, size, elevation, and geological history of the islands are described. To determine the degree of disharmony of the island floras, they are analyzed in comparison with selected California mainland floras. The degree of richness of the island floras is discussed in relation to size of the islands, proximity to the mainland, and other variables.

Such phenomena of island life as the immigrant pattern of vertebrate distribution, relict *versus* autochthonous endemism of plants and animals, insular gigantism, continuous flowering, high degree of hybridization, vulnerability, and loss of dispersibility in island species are considered in reference to the California Islands. Some suggestions as to available facilities on the islands and persons or institutions to contact are given in an epilogue.

Off the Pacific coast of southern California and Baja California, Mexico, lie the islands variously called the Channel Islands or California Offshore Islands and the Baja California Islands or, collectively, the California Islands. Although they are in no sense tropical, they are worthy of mention in this symposium because they are a good example of a fringing archipelago and because they illustrate many of the insular phenomena that one might otherwise have to travel far to tropical areas to study. Some of them are quite accessible from the heavily populated areas of southern California, and some of them have been rather thoroughly studied by biologists. Although they are, thus, rather well known to California biologists, they are surprisingly little known to non-Californians. It is hoped that this short discussion of them and of some of their insular characteristics will create more interest in them among those biologists concerned with evolutionary and environmental phenomena.

The Southern California and Baja California Islands consist of 16 major islands or island groups spread over some 500 miles between Point Conception, California, and Punta Eugenia, Baja California, Mexico (Fig. 1). From east to west the Northern Channel Islands are Anacapa, Santa Cruz, Santa Rosa, and San Miguel. The Southern Channel Islands are San Nicolas, Santa Barbara, Santa Catalina, and San Clemente Islands. The Baja California Islands include Los Coronados just south of San Diego, Todos Santos off Ensenada, San Martin off San Quintin, San Gerónimo south of El Rosario, the San Benitos, Cedros, and Natividad off Punta Eugenia, and Guadalupe 157 miles off the Baja California peninsula.

In order of size, with area in square miles, the islands are: Cedros (134), Guadalupe (98), Santa Cruz (96), Santa Rosa (84), Santa Catalina (75), San

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Clemente (56), San Nicolas (22), San Miguel (14), Natividad (2.8), San Benito (2.5), Anacapa (1.1), Santa Barbara (1.0), Los Coronados (1.0), San Martin (0.9), Todos Santos (0.5), and San Gerónimo (0.2). Their distances from the mainland, in statute miles, are: San Martin (3), Todos Santos (4), Natividad (5), San Gerónimo (6), Los Coronados (8), Anacapa (13), Cedros (14), Santa Cruz (19), Santa Catalina (20), San Miguel (26), Santa Rosa (27), Santa Barbara (38), San Benito (41), San Clemente (49), San Nicolas (61), and Guadalupe (157). All these figures are from a summary by Philbrick (1967). The highest elevations on the largest islands, in feet, are: Guadalupe (4,257), Cedros (3,950), Santa Cruz (2,165), Santa Catalina (2,069), San Clemente (1,965), Santa Rosa (1,574), and San Nicolas (907).

Geological History

Also most pertinent to an understanding of the biology of these islands is the probable geological history of the islands and their biota. The following geological information was gleaned from various sources, but especially from Axelrod (1967*b*), Orr (1967), Reed (1933), Smith (1933), Valentine and Lipps (1967), and Weaver and Doerner (1967).

The islands appear to have had rather diverse origins. All of them, except Guadalupe, are probably of continental origin, for they appear to be the emergent tops of elongated mountain ridges separated by deep submarine basins on the broad continental borderland. The four Northern Channel Islands, an east-west chain, are disjunct segments of the Santa Monica Mountains, or Anacapia, on the south edge of the California Transverse Ranges. They have had an active history of emergence and submergence. Western Anacapia may have formed the northern edge of the larger ancient land mass known as Catalinia, which included the present Southern Channel Islands and the Palos Verdes Hills, a former island now joined to the mainland. Catalinia probably appeared in Cretaceous time. It underwent intermittent periods of uplift and submergence, and it may occasionally have been connected with the mainland. It unloaded great quantities of sediments into a seaway to the east during Miocene time, and its basin and range topography is due to block-faulting, which probably dates in part from the Miocene.

Anacapia may have had a pre-Cenozoic origin as reflected in its granitic core intruded into metamorphic rocks that are overlain by Cretaceous and pre-Pliocene sedimentary and volcanic rocks, which in turn are capped by Pleistocene terrace formations. Apparently Anacapia was joined to the mainland in Oligocene, Miocene, Pliocene, and late Pleistocene times, but these emergences were separated by submergences, particularly in Miocene and Pleistocene times, that may have nearly or completely destroyed terrestrial biotas. Thus, the present biota of the Northern Channel Islands may largely date from pre-Illinoian time in the Pleistocene when the northern islands were connected to the mainland as an east-west trending peninsula. Previous to this time, as suggested by wave-cut platforms on the top of Farrel Mountain on Santa Rosa, to near the top of Green Mountain on San Miguel, and to 1,800 feet on the north side of Santa Cruz, only the highest peaks of one

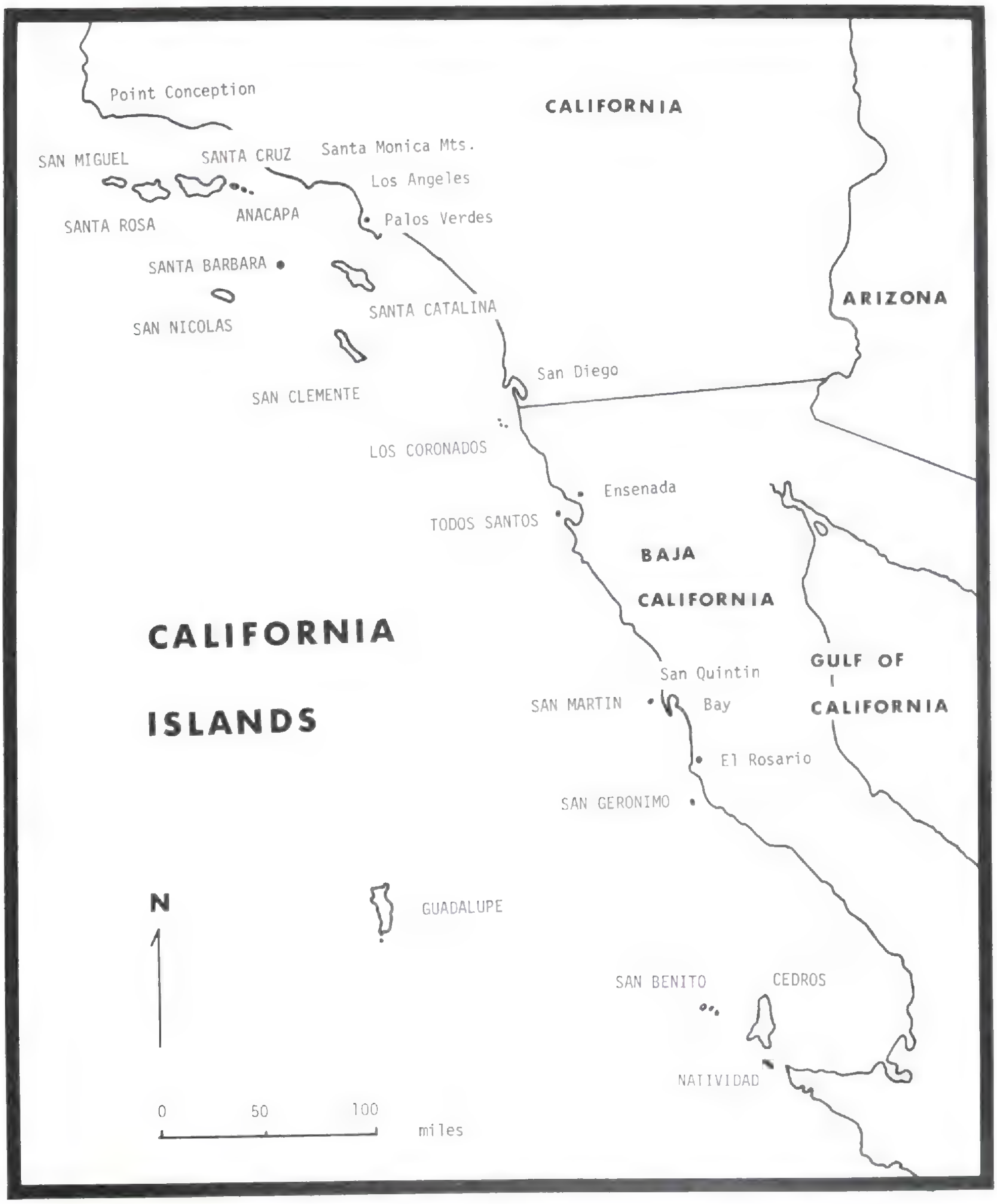

FIGURE 1.—Outline map of the California Islands.

island, Santa Cruz, may have been above water. Fossil remains of dwarf mammoths in Pleistocene terrace deposits on Santa Cruz, Santa Rosa, San Miguel, and San Nicolas Islands (D. E. Savage & Downs, 1954) surely require terrestrial connections of these islands with each other and with the mainland through the Anacapas during the Pleistocene, perhaps a half million years ago. By Illinoian time the northern islands were cut off from the mainland. There is evidence that aboriginal man butchered and cooked a dwarf mammoth on Santa Rosa some 27,000 years ago (Orr, 1967). During the Iowan or lower Wisconsin glacial stages from about 11,000 to 20,000 years ago, lowered sea levels permitted

the connection of the Northern Channel Islands with each other but not with the mainland.

The geological history of the Southern Channel Islands is somewhat different. It is likely that the biotas of all of them have arrived over water. San Nicolas lies on a shallow submarine ridge running southeast from Santa Rosa and may have been connected to it terrestrially in the Pleistocene, as suggested by the fossil remains of the dwarf mammoth on San Nicolas. However, marine terrace deposits covering much of the central and northwestern portions of the island indicate total submergence in the late Pleistocene (Foreman, 1967). The much smaller and lower Santa Barbara Island was presumably also completely submerged at that time. Surf-cut terrace platforms, from sea level to nearly 2,000 feet, are also conspicuous on San Clemente, Santa Catalina, and the Palos Verdes Hills. On most of the islands they bear fossiliferous marine sediments. Radiometric age estimates suggest that the terraces on the Palos Verdes Hills range in age from about 380,000 to 120,000 years before the present. The higher terraces on the islands may be considerably older, even early Pleistocene in age. The nearly 20 distinct wave-cut terraces extending to 1,500 feet on San Clemente and the rather flat plateau-like summit area (highest elevation 1,965 feet at Thirst) would seem to leave little, if any, of that island above water at its greatest submergence. Similarly, the marine terraces to about 1,700 feet on Santa Catalina, the nearly horizontal line of the main ridge at about 1,550 feet, and the rounded summit elevations suggest prolonged marine abrasion during Pleistocene time. Little if any of the island could have remained above water from the Pliocene emergence. This submergence, along with the great depth of the San Pedro Channel separating Santa Catalina from the Palos Verdes Hills, precludes migration overland to the island during the Pleistocene.

Of all the California Islands, only Guadalupe is clearly oceanic. Volcanic in origin, it rises some 15,000 feet from the sea bed, 157 miles from the peninsula of Baja California. Depths of some 12,000 feet lie between the island and the peninsula. The oldest lava flow on the island is reported to be about 7 million years old (Hubbs, 1967). One can hardly question the over-water origin of its biota. The other Baja California Islands, except the San Benitos, are within a few miles of the coast of Baja California, and probably were connected to the peninsula during the lowest sea level of the Wisconsin glacial stage, perhaps 20,000 years ago. Little attention will be given to these onshore islands in the following discussion.

DISHARMONIC ISLAND BIOTAS

Disharmony of insular biotas has been discussed by many students of island life, most recently by Thorne (1963, 1965), Carlquist (1965), and Balgooy (1969). An island that is a recently separated continental fragment may be expected to have a biota nearly as balanced, rich, diverse, and representative as that of an area of comparable size and diversity of habitat on the adjacent continent. An isolated oceanic island, on the contrary, may be expected to have a depauperate, disharmonic biota lacking numerous groups of organisms ill-adapted to long-

distance dispersal over water. Numerous ecological niches on such islands remain empty or are filled by organisms not normally found in similar continental niches. Comparison of the biota of an island with that of a similar area of the adjacent mainland should suggest whether the insular biota came over water or remains from a former continental connection. A quick examination of the present biotas of the California Islands, at least the offshore islands, suggests that they are mostly depauperate aggregations of plants and animals that have reached the islands by chance over-water dispersal. The floras of Santa Cruz and Santa Rosa Islands include remnants of a once richer continental flora. This last conclusion is supported by the late Pleistocene Willow Creek flora of Santa Cruz Island, which included such woody plants as *Pseudotsuga* Carr., *Cupressus goveniana* Gord., *Ceanothus thyrsiflorus* Esch., *Cornus californica* C. A. Mey., *Garrya elliptica* Dougl., and *Myrica californica* Cham. & Schlecht. (Axelrod, 1967*b*), all now vanished from the present insular flora.

The area of mainland southern California most nearly similar in size and topography to the Northern Channel Islands and Santa Catalina is the Santa Monica Mountains, or Eastern Anacapia, which is separated from Western Anacapia by the Santa Barbara Channel. Table 1 compares the flora of these mountains with floras of other California mainland areas, mostly along the moister central coast, and of various of the better known California Islands. The data for

TABLE 1. Statistical summary of indigenous taxa in selected California floras.

	Area in Square Miles	Families	Genera	Species, Subspecies, Varieties & Hybrids
A. MAINLAND AREAS				
1. Monterey County	3,324	105	433	1,422
2. Santa Cruz Mountains (San Francisco and Santa Cruz Counties)	1,386	108	445	1,246
3. Marin County	529	106	410	1,010
4. Santa Monica Mountains (Los Angeles and Ventura Counties, in part)	320	93	312	640
5. Santa Rosa Plateau (Riverside County, in part)	70	82	241	409
6. San Francisco County	45	91	304	661
7. San Bruno Mountains (San Francisco and San Mateo Counties, in part)	4.7	69	228	384
B. CALIFORNIA ISLANDS				
1. Cedros	134	56	173	205
2. Guadalupe	98	51	127	167
3. Santa Cruz	96	70	237	420
4. Santa Rosa	84	65	212	340
5. Santa Catalina	75	75	237	407
6. San Clemente	56	54	166	239
7. San Nicolas	22	32	71	106
8. San Miguel	14	39	110	190
9. Santa Barbara	1	26	54	65

the table were gleaned from the following sources: for Monterey County, Howitt and Howell (1964); Santa Cruz Mountains, Thomas (1961); Marin County, J. T. Howell (1949); Santa Monica Mountains, Raven and Thompson (1966); Santa Rosa Plateau, Lathrop and Thorne (1968) and Thorne and Lathrop (1969); San Francisco County, J. T. Howell, Raven, and Rubtzoff (1958); San Bruno Mountains, McClintock and Knight (1968); California Islands in general, Eastwood (1941) and Raven (1967); Cedros Island, Moran (1967; personal communication, 1970); Guadalupe Island, Eastwood (1929), J. T. Howell (1942) and Moran (1951, 1967, 1969; personal communication, 1970); Santa Catalina Island, Thorne (1967, 1969); San Clemente Island, Raven (1963) and Thorne (1969); San Nicolas Island, Foreman (1967); and Santa Barbara Island, Dunkle (1950) and Philbrick (1969).

Among the harmonic mainland floras there is an expected decrease in richness of flora with decrease in area at least with reference to the maritime floras of central California. The two southern California floras, for the Santa Monica Mountains and Santa Rosa Plateau, are considerably less rich for their size, presumably because of more arid climate and less ecological diversity. Among the insular floras, those of the larger islands closest to the mainland, Santa Cruz, Santa Rosa, and Santa Catalina, are relatively harmonic. Santa Cruz and Santa Rosa Islands have relatively rich floras and a larger number of tree and shrub species than Santa Catalina or San Clemente Islands. Among the more significant of these woody plants are: *Pinus muricata* D. Don (including *P. remorata* Mason), *P. torreyana* Parry *ex* Carr., *Acer macrophyllum* Pursh, *Arbutus menziesii* Pursh, four species of *Arctostaphylos* Adans., *Berberis (Mahonia) pinnata* subsp. *insularis* Munz, an undescribed *Garrya, Pickeringia montana* Nutt., many species of *Quercus,* including *Q. agrifolia* Neé, *Q. wizlizenii* var. *frutescens* Engelm., *Q. douglasii* H. & A., *Ribes malvaceum* Sm., *R. thacherianum* (Jeps.) Munz, and *Vaccinium ovatum* Pursh. These plants reflect moister conditions on the Northern Channel Islands and perhaps also suggest the retention of some species from the period of Pleistocene connection with the mainland.

The relatively harmonic flora of Santa Catalina more likely results from its close proximity to the mainland, only 20 miles off the Palos Verdes Hills, rather than from any former terrestrial connections, which geologically appear most unlikely since the early Pleistocene rise of the island. It lacks all the woody species listed above for Santa Cruz and Santa Rosa Islands.

The floras of the outer islands, such as San Clemente, San Nicolas, Santa Barbara, and San Miguel, are clearly depauperate and unbalanced. However, most disharmonic of all is the flora of the isolated volcanic oceanic island of Guadalupe despite its great age and relatively large size and high elevation. It presumably had a very depauperate flora even before its present devastation by goats. The relatively poor flora of the onshore Isla de Cedros is probably due to the rather arid climate of the island and of the adjacent mainland.

Various attempts have been made to correlate richness of flora with size of island. Too many variables, however, make such efforts rather futile. An analysis of the California Islands shows that in addition to size, other, often more im-

portant, factors are zonal climate, proximity to the mainland or to other large high islands nearer the mainland, elevation and topographic diversity, ecological diversity (as affected by topographic diversity, elevation, precipitation, and soil types) of the island and the adjacent continent, age of the island, and direction of currents, winds, and storms in conjunction with direction of the island from the continent or nearest high islands.

Immigrant Pattern of Distribution

As explained rather thoroughly by Darlington (1957), a fringing archipelago receives its vertebrate animals from the adjacent continent in approximate proportion to their vagility, *i.e.*, their dispersibility, and in an orderly way along the probable routes of immigration into the islands. Birds and bats are relatively numerous and little if at all differentiated from mainland populations. Lizards are well represented among the herpetofauna. Amphibians and terrestrial mammals, mostly small, are poorly represented. Most of the relictual endemic vertebrates will be on the islands closest to the mainland, except in the more vagile groups, wherein the relicts tend to be on islands farthest from the mainland.

In regard to these characteristics, as well as to others, the California Islands fit well Darlington's definition of a fringing archipelago. Birds and bats, and the marine pinnipeds (seals and sea lions), are very well represented and are seldom recognizably distinct from the mainland populations. Of 15 non-marine mammals known to be indigenous on the California Islands (Bloeker, 1967), nine species are bats. The other six are a depauperate assemblage of small mammals that must have reached the islands over water as waifs. Of the depauperate herpetofauna of 28 reptiles and amphibians (J. M. Savage, 1967), all but four are found also on the mainland, mostly adjacent to the islands. The 13 lizards are relatively well scattered over the more accessible California Islands, but only two have reached the more isolated San Nicolas and San Clemente and only one the small isolated Santa Barbara Island. The eleven snakes are restricted to Santa Cruz, Santa Catalina, and the onshore islands of Baja California. The four amphibians, one frog and three salamanders, are known only from the Northern Channel Islands, Santa Catalina, Los Coronados, and Todos Santos Islands. No indigenous reptiles, amphibians, or mammals are reported from the oceanic island of Guadalupe, which, however, did formerly have eight endemic species or subspecies of birds (Moran & Lindsay, 1950). The distribution of the few vertebrate relicts will be discussed below.

Relict Endemism

The outstanding feature of the California Islands is their high percentage of relict endemics. As a fringing archipelago they should be rich in endemics that have been eliminated from mainland habitats. Autochthonous endemics, on the other hand, should be relatively few and poorly marked. This is indeed the case. No family of plants is endemic to the California Islands though one of the two species of Crossosomataceae, *Crossosoma californicum* Nutt., is restricted to Santa

Catalina, San Clemente, and Guadalupe Islands. Four monotypic genera are endemic to the islands, *Hesperelaea* A. Gray (Oleaceae) and *Baeriopsis* Howell (Asteraceae) on Guadalupe, *Munzothamnus* Raven (Asteraceae) on San Clemente, and *Lyonothamnus* A. Gray (Rosaceae) on the larger Channel Islands. The *Hesperelaea* is now apparently extinct. Considering only Guadalupe and the Channel Islands there are 119 species and subspecies (or equivalent varieties) of seed plants restricted to the islands, with 32 of these endemic to Guadalupe Island. Thirteen are restricted to San Clemente, nine to Santa Cruz, seven to Santa Catalina, five to Santa Rosa, and two each to San Nicolas and Santa Barbara Islands. The remaining 50 are distributed on two or more islands, with 20 in the Southern Channel Islands (many also on Guadalupe), 13 in the Northern Channel Islands, and 17 in both groups. A dozen or more maritime species or subspecies are nearly restricted to the islands but still retain a foothold on the mainland of southern or Baja California. More detailed information about the endemic seed plants on the Channel Islands and Guadalupe may be found in Raven (1963, 1967) and Thorne (1967, 1969).

One might well ask why we think that these island endemics are mostly relicts and not island autochthons. For many of the endemics we must rely upon inference and rather circumstantial evidence. However, the dozen near-endemics mentioned above, most of them such distinctive plants as *Coreopsis gigantea* (Kell.) Hall, *Eriogonum grande* Greene, *Eriodictyon traskiae* Eastw., *Hemizonia greeneana* Rose, *Prunus ilicifolia* subsp. *lyonii* (Eastw.) Raven, *Salvia brandegei* Munz, and *Senecio lyonii* A. Gray, illustrate well plants that would be island endemics if their limited mainland representation should be wiped out by further desiccating change in the mainland climate or further disruptive activity by man. The limited fossil record is quite helpful in supplying fossilized remnants from interior California and Nevada of Miocene and Pliocene equivalents of such noteworthy woody island endemics or near endemics as *Ceanothus arboreus* Greene, *C. megacarpus* subsp. *insularis* (Eastw.) Raven, *Cercocarpus traskiae* Eastw., *Lyonothamnus floribundus* subsp. *asplenifolius* (Greene) Raven, *Prunus ilicifolia* subsp. *lyonii,* and *Quercus tomentella* Engelm. Several of these have related species in the uplands of southern Mexico (Axelrod, 1967*a,* 1967*b*).

There are also relict endemic species among the terrestrial vertebrates. Of the four endemic reptiles (J. M. Savage, 1967), three species endemic to Cedros Island are merely insular derivatives of mainland taxa. One endemic lizard, restricted to the outer islands of San Nicolas, Santa Barbara, and San Clemente, is, however, a primitive night lizard of the genus *Klauberina.* The three remaining related genera of the family Xantusiidae are found in arid or semi-arid southwestern North America and tropical Middle America and Cuba. A fifth genus is known from the Oligocene of Wyoming. One species of the salamander genus *Batrachoseps* is relict in a few isolated populations on Santa Cruz Island, the Monterey Peninsula, the southern Sierra Nevada, and the Sierra San Pedro Martir of Baja California. The rest of the amphibians and reptiles are vagile forms that have probably populated the islands by random over-water dispersal during late Pleistocene or Recent time.

The only endemic species of mammal on the islands is the Channel Islands fox, a diminutive gray fox, *Urocyon littoralis,* on the six largest Channel Islands. It appears to be a relict species whose closest relatives are three species of similarly small, gray foxes of Yucatan, Mexico, and Guatemala. These all appear, according to Bloeker (1967), to be more closely related to each other than any of them is to the common mainland gray fox, *Urocyon cinereo-argenteus.* Two of the most distinctive endemic mammals of the islands are known only from the late Pleistocene fossil record, the giant mouse, *Peromyscus nesodytes,* of the northern Channel Islands and the dwarf mammoth, *Mammuthus exilis,* of the Northern Channel Islands and San Nicolas. This last species was apparently hunted to extinction by the early aboriginal inhabitants of the northern islands. It is the one organism known from the California Islands that would seem to require former land connections to the mainland and between the islands it occupied.

Autochthonous Endemism

The California Islands, like most fringing archipelagos, function primarily as refugia for relicts rather than as evolutionary factories. They can in no way match such centers of evolution as the oceanic Hawaiian and Galapagean archipelagos. None the less, there has been some evolution on the islands. The deer mouse, *Peromyscus maniculatus,* is the most widely distributed and abundant mammal on 12 of the Channel Islands. It has radiated mildly into eight insular subspecies that occupy every habitat from the sandy beaches and rocky cliffs to the highest mountain tops (Bloeker, 1967). The island fox, *Urocyon littoralis,* has formed races on the six largest Channel Islands. The adorned shrew, *Sorex ornatus,* and California ground squirrel, *Spermophilus beecheyi,* have each developed a geographic race on Santa Catalina distinct from the mainland races. The big-eared harvest mouse, *Reithrodontomys megalotis,* has developed insular subspecies on Santa Catalina and Santa Cruz; and the spotted skunk, *Spilogale gracilis,* has evolved an insular subspecies on Santa Cruz and Santa Rosa. The Santa Cruz jay seems to be the one bird on the Channel Islands that may have differentiated subspecifically on the islands (T. R. Howell, 1967). The amphibians and reptiles perhaps evolve more slowly, for no subspeciation on the Channel Islands is mentioned by J. M. Savage (1967).

Autochthonous evolution on the islands is somewhat harder to prove among the seed plants. Carlquist (1965) has submitted a good probable example of adaptive radiation by flowering plants on the California Islands with his discussion of the shrubby tarweeds of the section *Zonamra* of the genus *Hemizonia* DC., whose species are largely restricted to these islands. Aside from the one fully mainland species, *H. minthornii* Jeps. of the Santa Susanna Mountains of Los Angeles and Ventura Counties, and colonies of *H. greeneana* Rose (recently described as subsp. *peninsularis* Moran, 1969) on Todos Santos and the coast of Baja California, the species are distributed over the islands, with *H. clementina* Brandegee on five of the Channel Islands, *H. streetsii* A. Gray on the San Benitos, and *H. frutescens* A. Gray *in* S. Wats., *H. greeneana* subsp. *greeneana,* and *H. palmeri* Rose on Guadalupe. Possibly, however, these five species did not evolve on the

islands, as suggested by the remnant populations of *H. greeneana* subsp. *peninsularis* on the Baja California coast. At least three of the island populations of *H. clementina,* however, show differences in leaves and vesture that suggest incipient subspeciation.

The genus *Dudleya* of the Crassulaceae may offer another example of radiation on the islands. Aside from eight species on the onshore islands of Baja California, there are at least nine species distributed on Guadalupe and the southern California Islands (Moran, 1959). *Dudleya blochmanae* subsp. *insularis* Moran, *D. candelabrum* Rose, *D. greenei* Rose, *D. guadalupensis* Moran, *D. hassei* (Rose) Moran, *D. traskiae* (Rose) Moran, and *D. nesiotica* Moran are restricted to the islands. *Dudleya virens* (Rose) Moran of Santa Catalina, San Clemente, and Guadalupe Islands has also one station on coastal bluffs at Point San Vicente of the Palos Verdes Hills, a former island. *Dudleya caespitosa* (Haw.) Br. & Rose is found on the Anacapa Islands as well as on the sea bluffs of the mainland from Monterey to Los Angeles Counties. Some of these species may well have differentiated on insular sea bluffs while others evolved on mainland sea bluffs. If *D. hassei* of Santa Catalina ever occurred on the mainland, it is surprising that it is not still here. At least at the Rancho Santa Ana Botanic Garden, Claremont, it is our most successful species of *Dudleya,* almost weedy in its aggressiveness. Aggressiveness certainly is not a characteristic usually associated with island endemics.

Another genus well developed on the islands is *Lavatera* L., the tree mallows of the Malvaceae. There are four California species, all insular. *Lavatera assurgentiflora* Kell. of the Channel Islands is most variable, each insular population appearing rather distinct and suggesting incipient subspeciation, as was the case in *Hemizonia clementina. Lavatera venosa* S. Wats. is restricted to San Gerónimo and San Benito Islands and rocks near the mouth of San Bartolomé Bay of Baja California (Moran & Lindsay, 1951). *Lavatera occidentalis* S. Wats. occurs on Los Coronados and Guadalupe and *L. lindsayi* Moran only on Outer Islet, with *L. occidentalis,* off Guadalupe. The susceptibility of these succulent-leaved plants to grazing animals, as illustrated on Santa Catalina where they now can be found only on the small islets of Indian and Bird Rocks, and on Guadalupe where they are also restricted to Outer Islet or inaccessible cliffs of the main island, may account for their almost total absence from the mainland. Presently *L. assurgentiflora,* along with the introduced Mediterranean species *L. arborea* L. and *L. cretica* L., is established along the mainland coast, especially in central and northern California.

The wild-tomato of the islands, *Solanum wallacei* (A. Gray) Parish, is probably derived from common ancestry with the mainland *S. xanti* A. Gray. It seems to have developed distinct subspecies on Guadalupe, on Santa Catalina, and on Santa Rosa and Santa Cruz Islands. *Solanum wallacei* subsp. *wallacei* of Santa Catalina has viscid, tawny-villous leaves, large purplish-blue corollas (2–4 cm broad), and dark purple berries 1.5–2.5 cm thick. *Solanum wallacei* subsp. *clokeyi* (Munz) Thorne of the Northern Channel Islands has less tawny and viscid foliage, smaller corollas (1.5–2 cm wide), and yellow berries 1–1.5 cm thick. The unnamed Guadalupe subspecies has leaves and flowers much like those on

Santa Catalina but smaller, yellow to plum-colored fruit like those of *S. wallacei* subsp. *clokeyi*.

Eriogonum giganteum S. Wats., the giant wild buckwheat of the Southern Channel Islands, though apparently a relict species, seems to have differentiated into three subspecies with *E. giganteum* subsp. *giganteum* on Santa Catalina, *E. giganteum* subsp. *formosum* (K. Brandgee) Raven on San Clemente, and and *E. giganteum* var. *compactum* Dunkle on Santa Barbara Island. Subspeciation seems to have occurred also in another relict, *Lyonothamnus floribundus* A. Gray. *Lyonothamnus floribundus* subsp. *floribundus*, with entire leaves, is known only from Santa Catalina. *Lyonothamnus floribundus* subsp. *asplenifolius* with pinnate-pinnatifid leaves, not found on Santa Catalina, is found to the south on San Clemente, to the north on Santa Cruz and Santa Rosa Islands, and extensively in the Miocene and Pliocene fossil record of mainland California and Nevada. *Lyonothamnus floribundus* subsp. *floribundus* is apparently unknown as a fossil. It seems to be a recent development and not a major genetic modification. The juvenile leaves are pinnate like those of the other subspecies, and injured or otherwise disturbed trees and branches produce pinnatifid or partially pinnate leaves intermediate between the leaves of the two subspecies.

Other taxa on the islands that show infraspecific or even specific insular differentiation are *Arctostaphylos* (see Wells, 1968), *Brodiaea* Sm. *(sens. lat.)*, *Camissonia guadalupensis* (S. Wats.) Raven, *Delphinum* L., *Eschscholzia* Cham., *Galium* L., *Lotus argophyllus* (A. Gray) Greene, *L. scoparius* (Nutt. *in* T. & G.) Ottley, *Malacothrix* DC., and *Mimulus* L.

Insular Gigantism

The tendency on oceanic islands toward prolonged growth, woodiness, and arborescence in taxa that are normally herbaceous is one of the most fascinating phenomena of island life. Particularly famous examples are the arborescent lobeliads of Hawaii and southern Polynesia; woody lettuces of the Juan Fernandez, Desventuradas, and Canary Islands; other rosette-shrub or tree composites of the Juan Fernandez, St. Helena, and Galapagos Islands; and shrubby or arborescent chenopods, amaranths, and four-o'clocks of Hawaii (Carlquist, 1965). Although the California Islands have not produced such spectacular plants, they nevertheless exhibit good examples of prolonged growth and woodiness. On Santa Catalina I found one specimen of *Eriogonum giganteum* subsp. *giganteum*, depicted in my flora of the island (Thorne, 1967), that had one stem 12 feet tall with a four-foot spread and a trunk diameter of 5 inches at 3 feet above the ground. *Eriogonum arborescens* Greene is also a sizable shrub. The islands even have their own woody lettuces, with *Munzothamnus blairii* (Munz & Johnst.) Raven, depicted in Raven's San Clemente flora (1963) growing on a vertical canyon wall, and its distant cousin on Guadalupe, *Stephanomeria guadalupensis* Brandegee. The *Munzothamnus* is a straggly shrub with stems to 7 cm in diameter and to 2 m long, often pendulous; the *Stephanomeria* is less massive with a stem to 3 or 4 dm high.

Insular woodiness is also well represented in other composite tribes. The shrubby *Hemizonia* tarweeds (Madiinae) of the California Islands have been dis-

cussed above. The remarkable *Coreopsis gigantea* (Heliantheae) is a rosette-shrub with tufts of much-dissected leaves borne at the ends of the stout fleshy stems up to 12 cm thick and 2 or 3 m tall. Guadalupe and the Channel Islands share it together with rocky bluffs and exposed dunes along the mainland coast from San Luis Obispo County to Los Angeles County. The Heleneae, perhaps not truly distinct from the Heliantheae, are represented by *Eriophyllum nevinii* A. Gray, a handsome shrub with leaves white-tomentose on both sides, of the Southern Channel Islands, and by *Perityle incana* A. Gray of Guadalupe Island. *Haplopappus canus* (A. Gray) Blake of Guadalupe and San Clemente and *H. detonsus* (Greene) Raven of the Northern Channel Islands belong to the Astereae; and *Senecio palmeri* A. Gray of Guadalupe and *S. lyonii* A. Gray of Santa Catalina and San Clemente, and of San Martin and adjacent Bahia de San Quintin of Baja California, to the Senecioneae.

Woodiness on the islands is by no means restricted to the Polygonaceae and Asteraceae. In the Papaveraceae, in addition to the expectedly woody *Dendromecon rigida* subsp. *rhamnoides* (Greene) Thorne and *D. rigida* subsp. *harfordii* (Kell.) Raven of the Channel Islands, there is a woody poppy or two on Guadalupe, *Eschscholzia (Petromecon) palmeri* Rose and *E. (Petromecon) frutescens* Greene. *Erysimum insulare* Greene (Brassicaceae) of Guadalupe's Outer Islet and the Northern Channel Islands and *Galium angulosum* A. Gray (Rubiaceae) of Guadalupe are woody-stemmed suffrutescent perennials. *Talinum guadalupense* Dudley (Portulacaceae) of Guadalupe is a succulent shrub with beautiful pink flowers, and *Galvesia speciosa* (Nutt.) A. Gray (Scrophulariaceae), the bush-snapdragon of Santa Catalina, San Clemente, and Guadalupe, is an arching or pendulous shrub on steep sea bluffs and canyon walls. Whether most of these unusually woody plants evolved on the islands or, more likely, under a moderate maritime climate along the mainland coasts would now be hard to determine. Several, like *Coreopsis gigantea, Senecio lyonii, Hemizonia greeneana,* and *Dendromecon rigida,* do occur on the mainland. And the shrubby *Euphorbia misera* Benth. is shared by the maritime desert scrub of the southern islands and the southern mainland and by the desert coasts of Sonora and the islands in the Gulf of California.

It may be pertinent to mention here that the harvest mouse, deer mouse, ground squirrel, and spotted skunk on the Channel Islands (Bloeker, 1967) and the Santa Cruz jay (T. R. Howell, 1967) are all larger than their mainland counterparts. The island fox is much smaller than the mainland gray fox, but, as stated above, it may be much more closely related to similarly diminutive gray foxes in Middle America. The extinct giant mouse, *Peromyscus nesodytes,* of the islands adds further weight to this apparent mild gigantism in small mammals. The extinct dwarf mammoth, *Mammuthus exilis,* of late Pleistocene time, however, was much smaller than its mainland counterpart, the imperial elephant, *Mammuthus imperator.* It calls to mind the extinct pygmy hippopotamus that was abundant on Madagascar during Pleistocene time. It would seem that restriction of space on islands leads to diminished size or extinction of larger mammals relict on them or reaching them over water, while permitting increase in size of the smaller mammals.

Continuous Flowering

The continuously temperate, maritime climate that allows prolonged growth among the island herbs also favors continuous or nearly continuous flowering among several of the evergreen shrubs. The mainland subspecies of tree poppy, *Dendromecon rigida* subsp. *rigida,* has a relatively brief flowering period, but the island subspecies, *D. rigida* subsp. *rhamoides* and *D. rigida* subsp. *harfordii,* seem to bloom almost continuously. This has been observed both among wild plants and among our plantings of mainland and island subspecies at the Rancho Santa Ana Botanic Garden. The bush-snapdragon, *Galvesia speciosa,* blooms continuously in our Garden also, as it presumably does on its island homes. *Lavatera assurgentiflora* and *Crossosoma californicum* have long blooming periods in the Garden, and perhaps many other less conspicuous island plants would prove, upon careful observation, to have similarly prolonged flowering.

Hybridization

The ability of island plants to hybridize freely has often been noted. Certainly the plants of the California Islands are no exception. One wonders why the island habitat leads to such promiscuity among the plants. There is surely some selective advantage from the increased variability brought into island populations by gene introgression (Carlquist, 1966). The oaks of Guadalupe and the Channel Islands are perhaps the most notorious hybridizers. *Quercus* × *macdonaldii* Green, a rather frequent, large, spreading tree on Santa Catalina, is apparently the hybrid offspring of *Q. dumosa* Nutt. and *Q. lobata* Neé. Less conspicous but abundant are the apparent backcrosses with both putative parent species. Trees of *Quercus chrysolepis* Liebm. on Mt. Orizaba, Santa Catalina, seem to show varying degrees of heavy to light introgression from nearby groves of the island oak, *Q. tomentella* Engelm. The extraordinary variability of the scrub oak, *Q. dumosa* Nutt., on the Channel Islands must in part derive from introgression from other species, especially from *Q. lobata* and less commonly from *Q. engelmanni* Greene and *Q. douglasii* H. & A. (Muller, 1967).

Hybridization is even more extreme among the native low-spreading or prostrate prickly-pears that abound over most of the Channel Islands. Hybridization among them and with the introduced mission cactus, *Opuntia ficus-indica* (L.) Mill., is so rampant and the variation pattern so complex that it is nearly impossible to identify most of the plants seen. The two primary indigenous species involved are *O. littoralis* (Engelm.) Cockerell var. *littoralis* and *O. oricola* Philbrick, though other species, as *O. phaeacantha* var. *discata* (Griffiths) Bens. & Walk. and "*O. demissa* Griffiths," may also be participating.

Other genera also seem to hybridize freely on Santa Catalina. Apparent hybrids between the evergreen sumacs *Rhus ovata* S. Wats. and *R. integrifolia* (Nutt.) Benth. & Hook. *ex* Rothr. seem to be rather frequent as do also those between *Dudleya virens* and *D. hassei.* Less frequent are the apparent hybrids between *Salvia apiana* Jeps. and *S. mellifera* Greene. At the one station found on Santa Catalina for the rare island endemic rock-rose *Helianthemum greenei* Robins. (Cistaceae) the more common *H. scoparium* Nutt. var. *vulgare* Jeps. was also

found with an apparent hybrid intermediate in appearance between the two putative parent species. Likewise at the only station for the nearly extinct and striking Catalina-mahogany, *Cerocarpus traskiae* Eastw. (Rosaceae), in a canyon on the Salta Verde, Santa Catalina, one or two of the few remaining trees appear to show genic introgression with *C. betuloides* var. *blancheae* (C. K. Schneid.) Little, which is also present in the canyon.

In a few instances hybridization on Santa Catalina seems to have "swamped out" one of the putative parents. I was unable to find any "pure" specimens of *Quercus lobata* despite the apparent abundance of hybrid offspring between it and *Q. dumosa*. *Q. chrysolepis* on Santa Catalina may in a few more generations be swallowed up genetically by *Q. tomentella*. *Cercocarpus traskiae* may similarly disappear into *C. betuloides* var. *blancheae*. The populations of *Ceanothus megacarpus* Nutt. (Rhamnaceae) on both San Clemente and Santa Catalina seem to represent a hybrid swarm between the mainland subsp. *megacarpus* and the insular subsp. *insularis* (Eastw.) Raven. The leaves resemble the latter more closely in size but are mostly alternate as in the former. The capsules vary from the conspicuously horned *megacarpus* types to the almost hornless *insularis* types. The bush monkey-flower, *Mimulus* (*Diplacus*) *puniceus* (Nutt.) Steud. (Scrophulariaceae) on Santa Catalina represents, according to McMinn (1951), "hybrid swarms which have probably resulted from the crossing and back-crossing" of *M. puniceus* with *M. longiflorus* (Nutt.) Grant. "Pure" *M. longiflorus* seems to have been "swamped out" by *M. puniceus*, for I could find no traces of it among the numerous and varied representatives of the bush monkey-flower on the island. Apparent hybrids between *M. longiflorus* and *M. flemingii* Munz are frequent on Santa Cruz Island with the putative parents.

In all fairness to mainland hybridization, one must admit that *Quercus, Opuntia, Diplacus, Salvia, Rhus, Dudleya, Ceanothus,* and other genera appear to be pretty promiscuous on the mainland also, though I have never observed the prevalence of hybridization in mainland populations that I have found in insular populations.

VULNERABILITY

A most unfortunate characteristic of insular plants and animals is their vulnerability. Under insular conditions there is usually rather complete protection from large predators and from large grazing animals. The waif origin of the biota leads to many open niches and a relatively low level of competition among the species present. This general freedom from the predators, grazers, browsers, and competitors that abound on adjacent continental land masses places no great selective value on the usual defences "built-in" to the genotypes of mainland plants and animals. The instinctive or "learned" wariness of animals on the mainland is often replaced on islands by a fearlessness that makes the animals ready prey for introduced mainland predators. The lack of timidity of the small island foxes on Santa Cruz, which stood unafraid and watched us with apparent curiosity and which are reputed to feed from the hands of visitors to the biological laboratory there, is one example of this phenomenon. Another is the indifference to man of the northern elephant seals, *Mirounga angustirostris,* on their hauling-out beaches

on the islands. Even the common green rattlesnake, *Crotalus viridis,* on Santa Catalina seemed quite unaggressive and usually rather indifferent to man, though I did not venture to handle it during several encounters on the island.

When predators like man, feral cats, and dogs are introduced to an island, the depredation on the animal life is rapid and often complete. The disappearance of the pigmy mammoth from the Northern Channel Islands is rather surely the work of aboriginal man. The commercial sealers of the early nineteenth century all but exterminated the northern elephant seal and the Guadalupe fur seal, *Arctocephalus phillippii townsendi.* Both have fortunately made phenomenal comebacks since they became legally protected by the Mexican and American governments in the early twentieth century. The sea otter, *Enhydra lutris,* was exterminated in the southern California islands by the fur-hunters, though a pitiful remnant did survive in the Monterey region. Now the protected California coastal population is increasing, and occasional stray otters are seen among the Northern Channel Islands. On many of the islands some or all species of ground-nesting bird have been exterminated by feral cats. The elimination of most of the endemic birds of Guadalupe Island has been attributed to such predators (Moran & Lindsay, 1950).

The devastation of the island floras by the white man and his introduced goats, sheep, and pigs has been pathetic. We can only surmise what the vegetation and floras must have been like before the advent of goats and sheep on Guadalupe, San Clemente, San Nicolas, parts of Santa Catalina, and the other islands. On Guadalupe numerous species have been eliminated. The monotypic genus *Hesperelaea* is apparently extinct, presumably cut for a goat corral (Brandegee, 1900). The groves of *Juniperus californica* Carr. reported by Palmer (*in* Watson, 1876) are gone. The species is presently represented by a few scraggly individuals (Moran, personal communication, 1970). No reproduction of the other tree species, as *Cupressus guadalupensis* S. Wats., *Pinus radiata* Don, *Erythea edulis* (Wendl.) S. Wats., and *Quercus tomentella,* is permitted by the goats. On Guadalupe these species seem to be doomed with the passing of the present generation of trees. Five species of the plants found on goat-free Outer Islet (Moran, 1967, 1969) two miles south of the main island, have never been found on the main island, though they were surely once there. The species of *Lavatera* mentioned above are prime examples of vulnerable plants (Brandegee, 1900) that can survive only on inaccessible cliffs or on goat-free rocks off the main islands.

After much intensive collecting on Santa Catalina by many botanists for many years, we have been unable in the last 25 or 30 years to recollect 43 (of 396) indigenous species found on the island by earlier botanists. Some of these plants, as is also true on the other islands, have not been seen since they were collected by the first botanists to visit the island. The succulent grass *Dissanthelium californicum* (Nutt.) Benth., reported by Palmer as most attractive to the goats, was collected just once each on Guadalupe, San Clemente, and Santa Catalina. It has presumably been eliminated by these voracious herbivores. Perhaps ten or more of the endemic flowering plants described from the California Islands have already been exterminated.

LOSS OF DISPERSIBILITY

Loss of dispersibility, characteristic in plants and animals on oceanic islands (Carlquist, 1965), is not expected among the biota of a fringing archipelago. Because of recent connections with the mainland or the relative ease of dispersal of plant and animal species to islands close to continental areas, there usually has been too little time for evolution by the island inhabitants toward loss of flight among birds and insects or increased seed size among the plants. Furthermore, the presumed constant influx of continental waifs may quickly "swamp out" or eliminate through competition the less aggressive populations of the same or related species or unrelated species occupying the same ecological niches. Thus, one would expect to find loss of dispersibility only, if at all, on the most ancient and isolated of the California Islands, Guadalupe. On Guadalupe there is one likely candidate that has suffered a loss of dispersibility for over water dispersal at least, through enlargement of its edible fruit. The Guadalupe palm, *Erythea edulis,* has a black, globose drupe that is 25–35 mm in diameter with soft pulp and a nutlet about 20 mm in diameter crosswise (Bailey, 1937). The closest relative geographically is the blue palm, *E. armata* S. Wats. of Baja California with fruits (11–) 18–24 mm long and nutlets usually about 15 mm in diameter. The closest species morphologically is *E. aculeata* Brandegee, the Sinaloa palm, with fruits 20–25 (–28) mm long and nutlets about 15 mm across. The other three mainland Mexican species also have smaller fruits and smaller, often thinner nutlets than *E. edulis.* T. R. Howell (1967) suggested that the now extinct Guadalupe caracara, *Polyborus lutosus,* might have fed on palm fruits and brought mainland seed to the island. I do not know whether ravens have ever formed part of the avifauna of Guadalupe, but about Santa Catalina Island they are most active and playful carriers of large fruits.

EPILOGUE

Should any of the readers of this paper wish to avail themselves of these insular refugia and laboratories of evolution, they might appreciate some information about available facilities on the islands and institutions or persons to approach. The University of California, Santa Barbara, now has a permanent field station on Santa Cruz Island. One can obtain information about the use of facilities there by writing to the Department of Biology, University of California, Santa Barbara, Goleta, California 93017. Similarly the University of Southern California has constructed a marine laboratory, the Marine Science Center, at the Isthmus on Santa Catalina Island. Since most of the island is owned by the Santa Catalina Island Company, Avalon, permission to collect and travel about the island should be sought from the Company. Mr. Douglas Propst, Ranch Superintendent for the Company, is an informed and enthusiastic naturalist and conservationist and has been most helpful to various scientists with projects requiring field study on the island.

The National Park Service, through its Channel Islands National Monument, has jurisdiction over Santa Barbara, San Miguel, and the Anacapa Islands. For information about visits to and studies on these islands one should get in touch

with the Chief Scientist, Channel Islands National Monument, Port Hueneme, California. To obtain permission to visit and travel about San Clemente Island, one should write to the Commanding Officer, United States Naval Ordnance Test Station, Pasadena Annex, California. San Nicolas is also under the jurisdiction of the United States Navy Department, Pacific Missile Range, Point Mugu, California 93041. Santa Rosa Island is privately owned, and permission to do scientific work there would have to be obtained from the owner, Mr. Al Vail.

The Baja California Islands belong to the Mexican Government and are less easy to visit. I can offer no helpful information about field work on them except to mention that Dr. Reid Moran, Curator of the Department of Botany, San Diego Natural History Museum, is the outstanding authority on their flora.

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DISTRIBUTION PATTERNS OF WEST INDIAN MOSSES

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Abstract

Distributions of West Indian mosses are analyzed in detail. The West Indies is an area of rather high species endemism, although a large portion of the species is common throughout much of tropical America. The relationship between the Greater Antilles and South America is much stronger than expected. The relationships of the West Indian species of *Pilotrichum* indicate some of the patterns of migration of mosses to the West Indies.

Using revisions, most of which have appeared in the last 25 years, I have summarized the distribution of 230 species of mosses which occur in the West Indies. The entire West Indian moss flora is much larger than this, of course. Crum and Bartram (1958) record 316 species from Jamaica. It is hoped that the selection of groups used in this survey reflects in a fairly representative fashion the kinds of patterns which the remaining mosses have. Revisions have been used because it is felt that, generally, the taxonomy is better in these than in floras. A few records for well-known species have been taken from island floras and check lists (*e.g.*, Crum & Bartram, 1958; Crum & Steere, 1957; Bartram, 1955).

The sources of data I have relied on are the following treatments of genera and families: Fissidentaceae (Grout, 1943); Dicranaceae (Williams, 1913*a*); Leucobryaceae (Williams, 1913*b*); *Calymperes* (Reese, 1961); Orthotrichaceae (Grout, 1946); Pterobryaceae (Arzeni, 1954); Neckeraceae (Wagner, 1951); Hookeriaceae (Welch, 1962, 1966, 1969), *Daltonia* (Bartram, 1931); *Pilotrichum* (Crosby, 1969).

A chart was made for the distribution of each species. The occurrence of each was recorded for all the major West Indian islands, Mexico, and the countries of Central and South America. In some cases it was possible to list only "West Indies," "Central America," or "South America." Thus the totals for some of the special tables may not agree with the total for the whole West Indies. Trinidad and Tobago were treated together and a record kept for them. These were eventually considered part of South America. For purposes of this discussion Mexico is part of Central America.

Table 1 summarizes the distribution of West Indian mosses. A small portion (*ca.* 1%) of the species are pan-tropical. Examples include *Fissidens asplenioides* Hedw. and *Octoblepharum albidum* Hedw. The species which occur in the West Indies and otherwise only in North America (*ca.* 4%) are of two kinds—those which have tropical affinities and barely reach North America, *e.g.*, *Calymperes nashii* Williams and *Cyclodictyon varians* (Sull.) O. Kuntze, and those which barely reach the tropics from the north, *e.g.*, *Orthotrichum anomolum* Hedw. The species which occur in the West Indies and North America as well as Central and South America make up 8% of the total. These are mainly species with tropical affinities which extend their range into the southeastern United States.

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TABLE 1. Distribution of West Indian mosses.

	Number of species	Percent of total
West Indies and		
Central America only	27	*12*
South America only	31	*13*
Central and South America	63	*27*
Central, South and North America	19	*8*
Central and North America	12	*5*
North America	8	*4*
Pantropical	2	*1*
Endemic	68	*30*
Total	230	*100*

Included among these are *Jaegerina scariosa* (Lor.) Arzeni, *Lepidopilum polytrichoides* (Hedw.) Brid., *Calymperes richardii* C. Müll. and *C. erosum* C. Müll. Some in this group, however, are elements which extend into the tropics from the north. *Leucobryum albidum* (P. Beauv.) Lindb. and *Dicranum scoparium* Hedw. are included here.

The number of species occurring in the West Indies and elsewhere only in Central America (12%) and elsewhere only in South America (13%) are about equal. When those which occur in both Central and South America (27%) are included, over half of the total moss flora is accounted for. The West Indian-Central American group, together with some species which extend also into northern South America, make up what may be called the Caribbean moss flora—those species which are generally distributed around the Caribbean area. Representative species are *Hookeriopsis guadelupensis* (Brid.) Jaeg., *Calymperes leryanum* Besch., and *Porotrichum cobanense* C. Müll.

A substantial portion of the flora is endemic to the West Indies. Several species of *Pilotrichum* are in this group and will be discussed later. Other endemics are *Crossomitrium cubense* P. Vard. & Thér., *Fissidens palmatus* Hedw., *Hookeriopsis fissidentoides* (Hook. f. & Wils.) Jaeg., and *Macromitrium harrisii* Par.

The West Indies may be divided into the Greater Antilles—Cuba, Jamaica, Hispaniola, Puerto Rico, and the Virgin Islands—and the Lesser Antilles. In this discussion only the high, recent, volcanic islands extending from St. Kitts south and east to Grenada were considered. Division into the Greater and Lesser Antilles is quite natural on geological grounds (Butterlin, 1956).

Table 2 summarizes the distribution of Greater Antillean and Lesser Antillean mosses. In this table those species which occur in North America have been included, but they are not distinguished in separate groups. The much greater size of the Greater Antillean flora (212 species) than the Lesser Antillean flora (105 species) is immediately evident. Endemism in the Greater Antilles is also higher than in the Lesser Antilles; 18% of the total number of Greater Antillean species is endemic, while only 12% of the total in the Lesser Antilles is endemic. As a whole 30% of the West Indies moss flora is endemic.

When the non-endemic portion of the moss flora is considered, the Greater Antilles are seen to have strong Central American affinities. Thirteen percent of

TABLE 2. Distribution of Greater and Lesser Antillean mosses.

	Number of species	Percent of total
Greater Antilles and		
Central America	27	*13*
Central and South America	34	*16*
Central America and Lesser Antilles	9	*4*
Lesser Antilles	18	*8*
Lesser Antilles, Central and South America	47	*22*
Lesser Antilles and South America	13	*6*
South America	27	*13*
Endemic to Greater Antilles	37	*18*
Total	212	*100*
Lesser Antilles and		
Central America	2	*2*
Central and South America	2	*2*
Central America and Greater Antilles	9	*9*
Greater Antilles	18	*17*
Greater Antilles, Central and South America	47	*45*
Greater Antilles and South America	13	*12*
South America	1	*1*
Endemic to Lesser Antilles	13	*12*
Total	105	*100*

the Greater Antillean species occur elsewhere only in Central America, while another 16% extend into South America. While these figures indicate migration from Central America to the West Indies, 13% of the non-endemic Greater Antillean species also occur otherwise only in South America. Migration from South America to the Greater Antilles appears to be just as likely as from Central America to the Greater Antilles. A small portion (6%) of the non-endemics extend through the Lesser Antilles to South America.

The picture in the Lesser Antilles contrasts sharply with that in the Greater Antilles. Only a very small portion of the non-endemic Lesser Antillean flora is either purely Central American (2%) or purely South American (1%). But again, migration from either Central or South America to the Lesser Antilles seems equally likely. The more generalized nature of the Lesser Antillean flora is reflected in the large portion (45%) which occurs through the Greater Antilles, Central and South America. When those species which occur in the Greater Antilles and Central America and in the Greater Antilles and South America are added, most of the non-endemic flora (66%) is accounted for.

The distribution of the 37 Greater Antillean endemics is given in Table 3. The general pattern is one of radiation from Cuba, with fewer species occurring on the more easterly islands. This pattern is apparent in the number of species which are confined to single islands, with Cuba having nine and Puerto Rico, the most easterly island, having none. The multiple island endemics are distributed in the same way. It should be pointed out that Hispaniola is by far the least well-known island in the Greater Antilles, and further exploration may upset this pattern.

TABLE 3. Distribution of Greater Antillean endemics.

	Number
Species endemic to individual islands	
Cuba	9
Jamaica	6
Hispaniola	1
Puerto Rico	0
Species occur on	
Cuba and Jamaica	6
Cuba, Jamaica and Hispaniola	3
Cuba, Jamaica, Hispaniola and Puerto Rico	3
Species bypass Cuba, occur on	
Jamaica and Hispaniola	1
Jamaica, Hispaniola and Puerto Rico	1
Species bypass Jamaica, occur on	
Cuba and Hispaniola	2
Cuba, Hispaniola and Puerto Rico	3
Species bypass Hispaniola, occur on	
Cuba, Jamaica and Puerto Rico	1
Species bypass Cuba and Hispaniola, occur on	
Jamaica and Puerto Rico	1
Total	37

In the Lesser Antilles the pattern for the 13 endemics appears to be one of radiation from the larger, north-central islands (Table 4). Guadeloupe and Martinique are the only islands with endemic species peculiar to themselves, with six and one species respectively. To the north and south fewer multiple island endemics are present.

This survey of distribution patterns indicates the overall affinities of the West Indian moss flora. The relationships of the various species involved and the distribution of their close relatives may indicate more about possible pathways of migration. I have recently revised the genus *Pilotrichum* and indicated what appear to be infrageneric relationships (Crosby, 1969). *Pilotrichum* consists of 20 known species, all of which are confined to the American tropics. Since 13 of the species occur in the West Indies, *Pilotrichum* may provide some clues concerning the origin and evolution of the West Indian mosses in general, or at least those species with tropical American affinities, which make up the largest part of the flora.

TABLE 4. Distribution of Lesser Antillean endemics.

	Number
Species endemic to individual islands	
Guadeloupe	6
Martinique	1
Species occur on	
Guadeloupe, Dominica and Martinique	3
Guadeloupe and Martinique	1
Species occur from	
Guadeloupe to Grenada	1
St. Kitts to Grenada	1
Total	13

Three species of *Pilotrichum* are fairly widely distributed. *Pilotrichum evanescens* (C. Müll.) Crosby and *P. bipinnatum* (Schwaegr.) Brid. occur from Central America to southern Brazil and on many of the West Indian islands. *Pilotrichum fendleri* C. Müll. is somewhat more restricted, occurring in Central and northern South America and on Jamaica. These species are representative of the large percentage of West Indian mosses which are broadly distributed in the American tropics.

The remaining ten *Pilotricha* which occur in the West Indies are endemic—five to the Greater Antilles and five to the Lesser Antilles. Since the leaves appear to reflect infrageneric relationships in *Pilotrichum,* they have been illustrated to represent the various endemic species (Fig. 1–2).

The closest relationships of the Greater Antillean endemics are mostly with other Greater Antillean endemics (Fig. 1). More distant relationships generally may be traced to species occurring in northern South America. Costal structure and phyllotaxy indicate that *P. compositum* (Hedw.) P. Beauv., which occurs on Jamaica and Cuba, has probably arisen from something like *P. lophophyllum* Sull., which occurs throughout the Greater Antilles. *Pilotrichum lophophyllum* appears to be quite close to *P. luciae* Crosby of Martinique, Lesser Antilles. These are both small species which share several costal features as well as having propagula borne in similar places. These three West Indian species show many similarities to *P. armatum* Broth. of Ecuador. *Pilotrichum armatum* possesses a more general 2/5 phyllotaxy, while the Antillean species all have 1/3 phyllotaxy. Thus a single progenitor from South America may have given rise to these species. Just how migration and change occurred is not clear. Immigration may have first taken

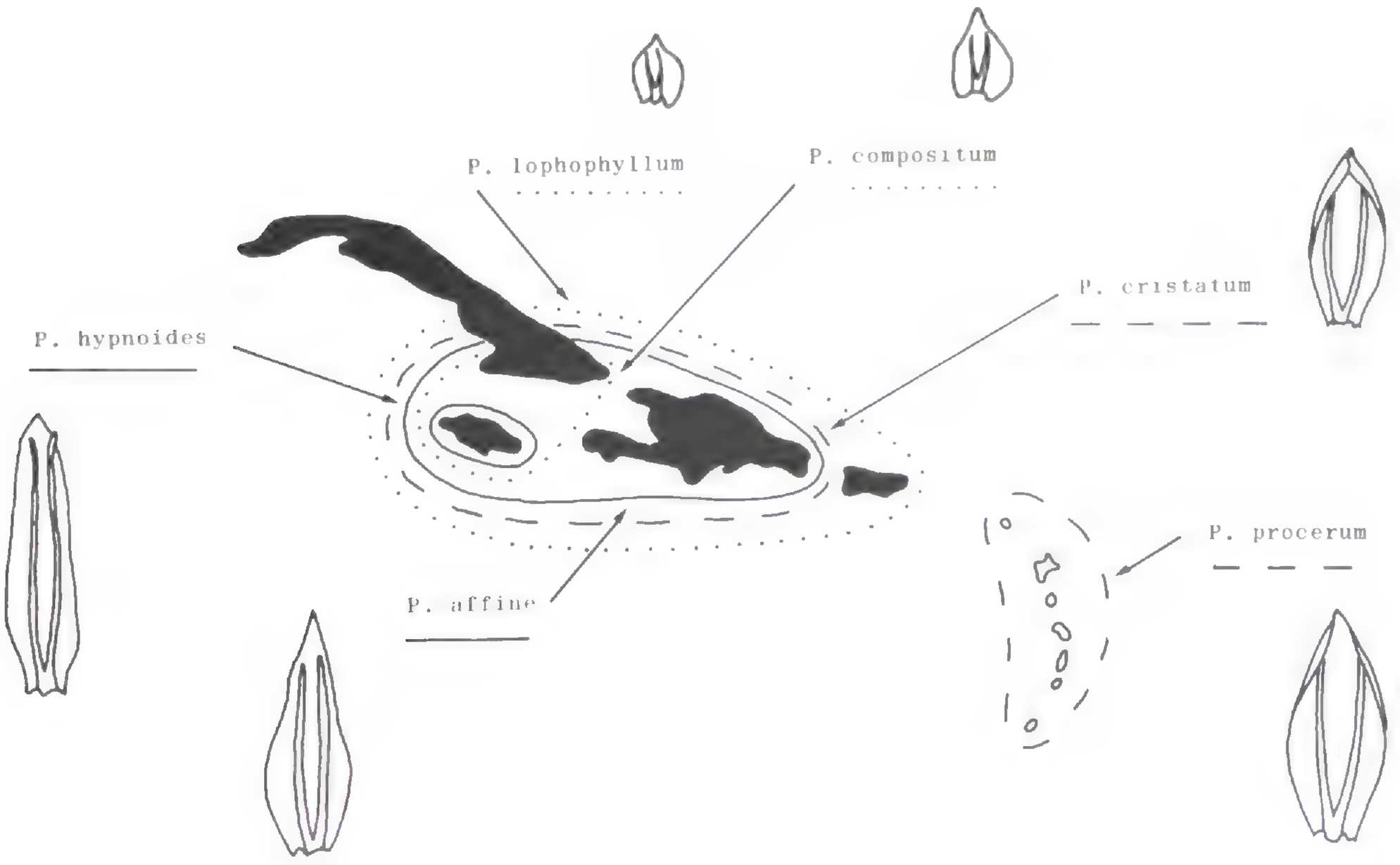

FIGURE 1.—Distributions and relationships of Greater Antillean species of *Pilotrichum*. The distributions of related species are shown with similar lines.

place to the Lesser Antilles, giving rise eventually to *P. luciae,* then further migration to the Greater Antilles, resulting in *P. lophophyllum* and *P. compositum*. It is equally plausible to suggest initial introduction and speciation in the Greater Antilles. Subsequent dispersal from the Greater Antilles to the Lesser Antilles of a *P. lophophyllum*-like plant could then account for *P. luciae*. The latter suggestion may be considered more likely due to the rather high percentage (13%) of species presently found only in the Greater Antilles and South America.

Pilotrichum cristatum Mitt. occurs on three of the Greater Antillean islands, Jamaica, Cuba, and Hispaniola. It is closest to *P. procerum* Mitt., which is the most widely distributed Lesser Antillean endemic. *Pilotrichum procerum* and *P. cristatum* are robust species with concave leaves and rather thick costae. *Pilotrichum longicaule* Broth. shares these characters, but seems to be closer to *P. procerum* than to *P. cristatum*. *Pilotrichum longicaule* is a northern South American species. *Pilotrichum cristatum* may then reflect migration through the Lesser Antilles from South America.

The remaining Greater Antillean endemic *Pilotricha, P. hypnoides* (Hedw.) P. Beauv. and *P. affine* (Hook.) Brid., share distinctive costal characters, and the areolation of their leaves is similar. The further relationships of these species are not clear. However, they may be derived from the broadly distributed *P. fendleri*. If so, they could be descended from plants originating in either Central or South America. (*Pilotrichum fendleri* is not known from the Lesser Antilles.)

The Greater Antillean *Pilotricha,* though not forming a closely knit group, are, individually, usually most closely related to other Greater Antillean species. More distant relationships are generally with South America.

Pilotrichum in the Greater Antilles also shows the radiation indicated for the flora as a whole, although Jamaica rather than Cuba has the largest total number of endemics. All five of the Greater Antillean endemic *Pilotricha* occur on Jamaica, and four occur on Cuba. To the east there are three on Hispaniola and only one on Puerto Rico.

In the Lesser Antilles radiation from the north-central islands occurs in *Pilotrichum* as in the endemic flora as a whole. All five endemic *Pilotricha* occur on Martinique and four are on Dominica and Guadeloupe. The extreme northern island, St. Kitts, has only one, while the extreme southern island, Grenada, has two.

The Lesser Antillean endemics show a pattern of relationships different from the Greater Antillean endemics (Fig. 2). Three of the five Lesser Antillean endemic species show close relationships to species which occur in northern South America. *Pilotrichum procerum* was discussed in connection with the Greater Antillean endemics. It is closest to *P. longicaule* of Ecuador, Venezuela, and probably Colombia. *Pilotrichum husnotii* Besch. of the northern Lesser Antilles and *P. ramosissimum* Mitt. of Central and northern South America share a distinctive branching pattern and have similar leaves as well. The third endemic, *P. divaricatum* Mitt., exhibits most dramatically the Lesser Antillean-South American relationship. *Pilotrichum divaricatum* occurs as far south as Grenada. It is very similar to *P. andersonii* Crosby on the basis of areolation, costal structure,

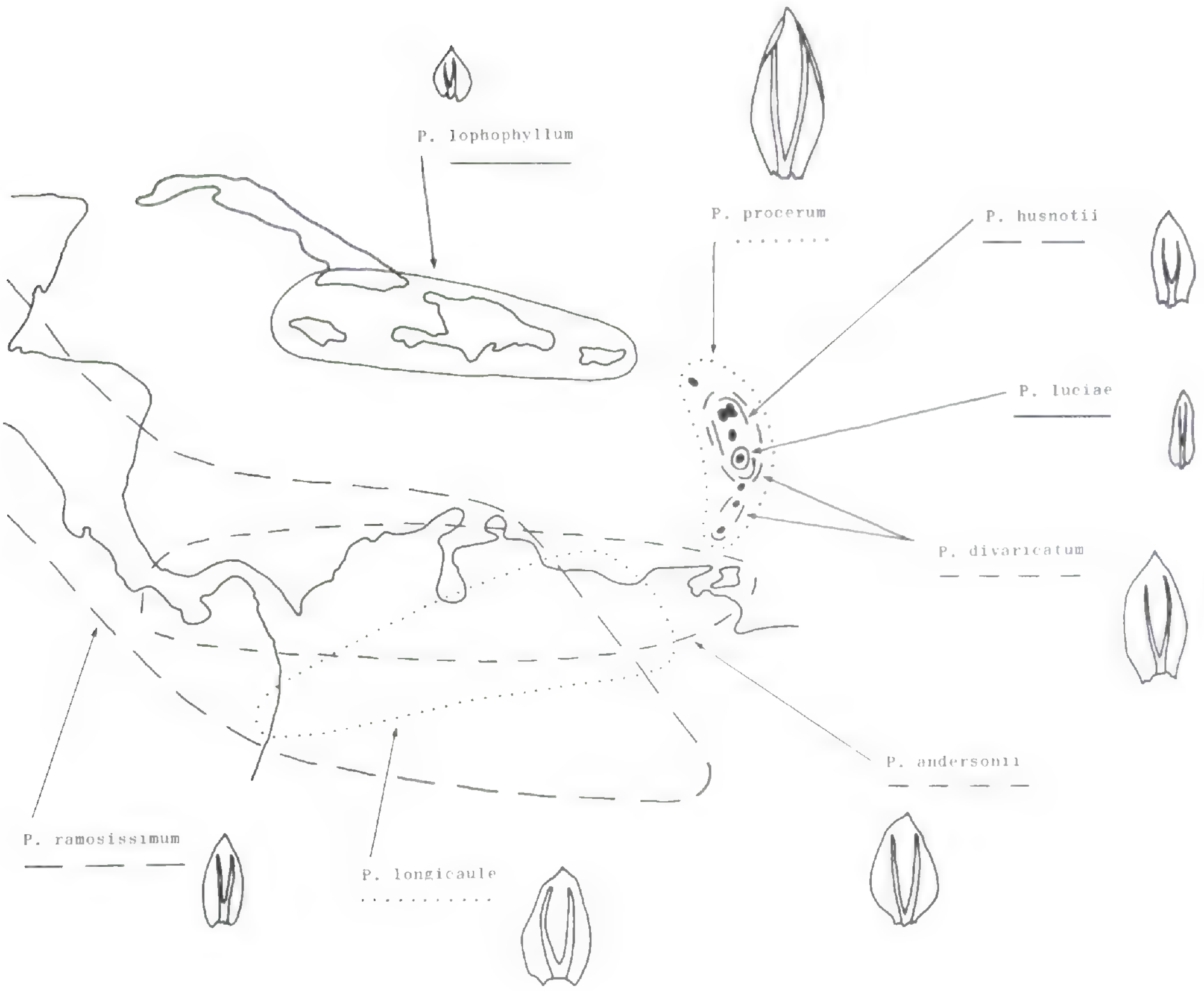

FIGURE 2.—Distributions and relationships of Lesser Antillean species of *Pilotrichum*. The distributions of related species are shown with similar lines. *Pilotrichum debile* is not illustrated.

and position of propagula. *Pilotrichum andersonii* occurs from Costa Rica across northern South America to Venezuela and reaches Trinidad.

Pilotrichum luciae has been discussed in connection with the Greater Antilles and probably indicates dispersal from that area rather than from South America. The fifth Lesser Antillean endemic, *P. debile* Besch., is not illustrated. Its closest relationships appear to be with *P. divaricatum*, and it is thus the only Lesser Antillean species whose closest relative is also in the Lesser Antilles.

The migration and evolution of *Pilotrichum* in the West Indies may be summarized as follows: In the Lesser Antilles three separate introductions from South America have given rise to *P. divaricatum*, *P. husnotii*, and *P. procerum*. Further evolution from a *P. divaricatum*-like species has produced *P. debile*. One introduction from the Greater Antilles accounts for *P. luciae*.

In the Greater Antilles two introductions produced four species—*P. lophophyllum* and *P. compositum*, originating from South America, and *P. hypnoides* and *P. affine*, originating from South or Central America. One introduction from the Lesser Antilles accounts for *P. cristatum*.

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DROSOPHILIDAE OF HAWAII

Hampton L. Carson[1]

The family Drosophilidae in Hawaii comprises over 500 species; all but 17 are endemic. A majority of species fall into two genera, *Drosophila* Fallen (324 species, 3 subgenera) and *Scaptomyza* Hardy (121 species, 7 subgenera). The remainder have been placed in endemic genera which are quite clearly either *Drosophila*-like (drosophiloid) or *Scaptomyza*-like (scaptomyzoid). Some species seem to combine certain characters of the two genera; this conclusion is based on internal anatomy, external morphology and behavior. Structural peculiarities are extraordinarily diverse, particularly in males. Characters include protruding eyes, modified mouthparts, and elaborate foretarsi, including bristle-like, spoon-like or forked adornments. Some species of *Drosophila* have extremely large body sizes.

Many species groups are informally recognized. The Maui complex has the greatest number of known species of drosophiloids (160) followed by Hawaii (98), Oahu (84), and Kauai (44); most are endemic to the specific islands from which they have been recorded. Most drosophiloids are found at high altitudes in areas of high humidity and breed on fermenting vegetable materials.

Nine oviposition sites on endemic plants are recognized of which leaves of *Cheirodendron* (46 species reared) and stems of *Clermontia* (18 species reared) predominate. In all, 32 endemic genera of plants are used. The leaf-breeding species are difficult to rear in the laboratory. Ecological niches include species which breed on spider eggs, decaying flowers and non-decaying plant hairs.

Polytene chromosome mapping has been carried out for 69 large drosophiloids (the picture-winged species group); all can be described in terms of a single set of arbitrary Standard gene orders despite morphological diversity of the species. *Drosophila primaeva* of Kauai has some polytene banding sequences which are recognizable in certain mainland forms, such as the predominantly Palearctic *D. robusta* group. As such sequences are altered by inversions in other picture-winged species, it appears that *D. primaeva* is chromosomally closer to the ancestral stock than any other Hawaiian species for which full information is available. Using this fact and the polytene chromosome relationships, theoretical evolutionary pathways for the subgroups of picture-winged flies have been constructed.

After Pliocene speciation episodes on Kauai, a minimum of 22 interisland founder events are proposed. These include two direct invasions of the Maui complex from Kauai; Oahu was by-passed and colonized later from the east. Nine colonizations of Hawaii took place in the late Pleistocene. Five of these cases show with great clarity that the ancestors came from Maui and that speciation resulted following the founder events.

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VEGETATION OF A GALAPAGOS ISLAND BEFORE AND AFTER AN ICE AGE

Paul A. Colinvaux[1]

A core from a crater lake on Isla San Cristóbal (Chatham Island) reaches a time shown by radiocarbon dating to be more than 48,000 years Before Present. A continuous pollen record of the last 10,500 years is preserved in the top three meters of sediment. Changes in the vegetation of the island are recorded for this period. But these changes represent alterations in the proportions of taxa present rather than invasions or extinctions.—The flora of the island did not alter much.

From 10,500 to more than 48,000 years B.P., the lake held no water, which seems to suggest that the climate was much drier than now. In ancient times (possibly during the last interglacial period) the lake did hold water. Peculiarities of its setting, a closed basin in the clouds, suggest that the climate of this early wet period was similar to that of postglacial times; but the pollen assemblages of the ancient lake sediments show striking differences to those of the postglacial period. In addition, a different species of *Azolla* occupied the lake and *Myriophyllum*, not known from the lake in postglacial time, was abundant. The two lake episodes were apparently separated by a climatic catastrophe sufficient to effect widespread extinction.

Although the pollen spectra of the ancient times were different from those of the postglacial period, all of the taxa represented (except the water plants) can be found in Galapagos surface samples from places other than near the modern lake. Since the climates of the two episodes are thought to be similar, this suggests that the vegetation of each episode has been much influenced by the fortunes of dispersal in the periods of early colonization.

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POLLEN MORPHOLOGY OF SAPROPHYTIC TAXA IN THE GENTIANACEAE[1]

SIWERT NILSSON[2] AND JOHN J. SKVARLA[3]

ABSTRACT

Pollen morphology of the saprophytic genera *Bartonia, Cotylanthera, Leiphaimos, Obolaria, Voyria,* and *Voyriella* (Gentianaceae) was studied by light and electron microscopy. *Bartonia, Obolaria,* and *Cotylanthera* are similar in fine structure, although the exine of the first two genera is reticulate and smooth in the latter genus. *Leiphaimos* and *Voyria* are indistinguishable but markedly different from all the other genera. *Voyriella* does not resemble *Voyria* or *Leiphaimos,* but appears similar to genera such as *Curtia* or *Enicostema* of Gilg's subtribe Gentianeae-Erythraeinae. Considerable intraspecific variation was noted within some of the taxa.

The Gentianaceae includes a number of saprophytic genera: *Cotylanthera, Obolaria, Bartonia, Voyria, Voyriella,* and *Leiphaimos* (Gray, 1868[4]; Johow, 1889; Knoblauch, 1894; Gilg, 1895; Figdor, 1896; Holm, 1897; Oehler, 1927). *Cotylanthera* has an Asiatic to Australasiatic distribution, *Bartonia* and *Obolaria* occur in eastern North America, and *Voyria, Leiphaimos,* and *Voyriella* are distributed in Central America, the West Indies, South America and tropical Africa.

The pollen morphology of these genera has been considered in earlier taxonomic, morphological and cytological studies (Gray, 1848; Gilg, 1895; Köhler, 1905; Oehler, 1927; Jonker, 1936*a*, 1936*b*; Erdtman, 1952; Raynal, 1967). Since questions concerning the taxonomic relationships of some of these genera still persist, we have re-evaluated the pollen by light microscopy and extended the study to include electron microscopy.

MATERIALS AND METHODS

Pollen was removed from herbarium specimens. Most samples were first processed by acetolysis treatment (Erdtman, 1960), while a few were soaked in 70% alcohol prior to further processing. For light microscopy only acetolyzed pollen was utilized. The pollen was mounted in glycerine jelly on microscope slides; coverslips were affixed and sealed with paraffin. Observations were made with a Leitz-Laborlux microscope. Size measurements generally are based on ten pollen grains.

For electron microscopy, acetolyzed and 70% alcohol treated pollen was stained with OsO_4 and uranyl acetate, or staining was omitted. Subsequent incorporation into agar, alcohol dehydration, and embedding in Araldite-Epon resins follows Skvarla (1966). Thin sections were made with diamond knives; section stains used were uranyl acetate, lead citrate, and saturated solutions of $KMnO_4$ in acetone. Observations and electron micrographs were made with a

[1] The authors extend their thanks to the Directors of the various herbaria for permission to collect samples of pollen. Special thanks are due to Professor F. P. Jonker for fruitful discussions on taxonomy and for verifying the specimens deposited at Utrecht, and also to Dr. W. Punt (Utrecht) for immeasurable help in supplying material and in some cases preparing slides. We are grateful to Mrs. Carole Pyle for assistance in preparing the manuscript.

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[4] Gray regarded *Eophylon* (*i.e. Cotylanthera*) as parasitic.

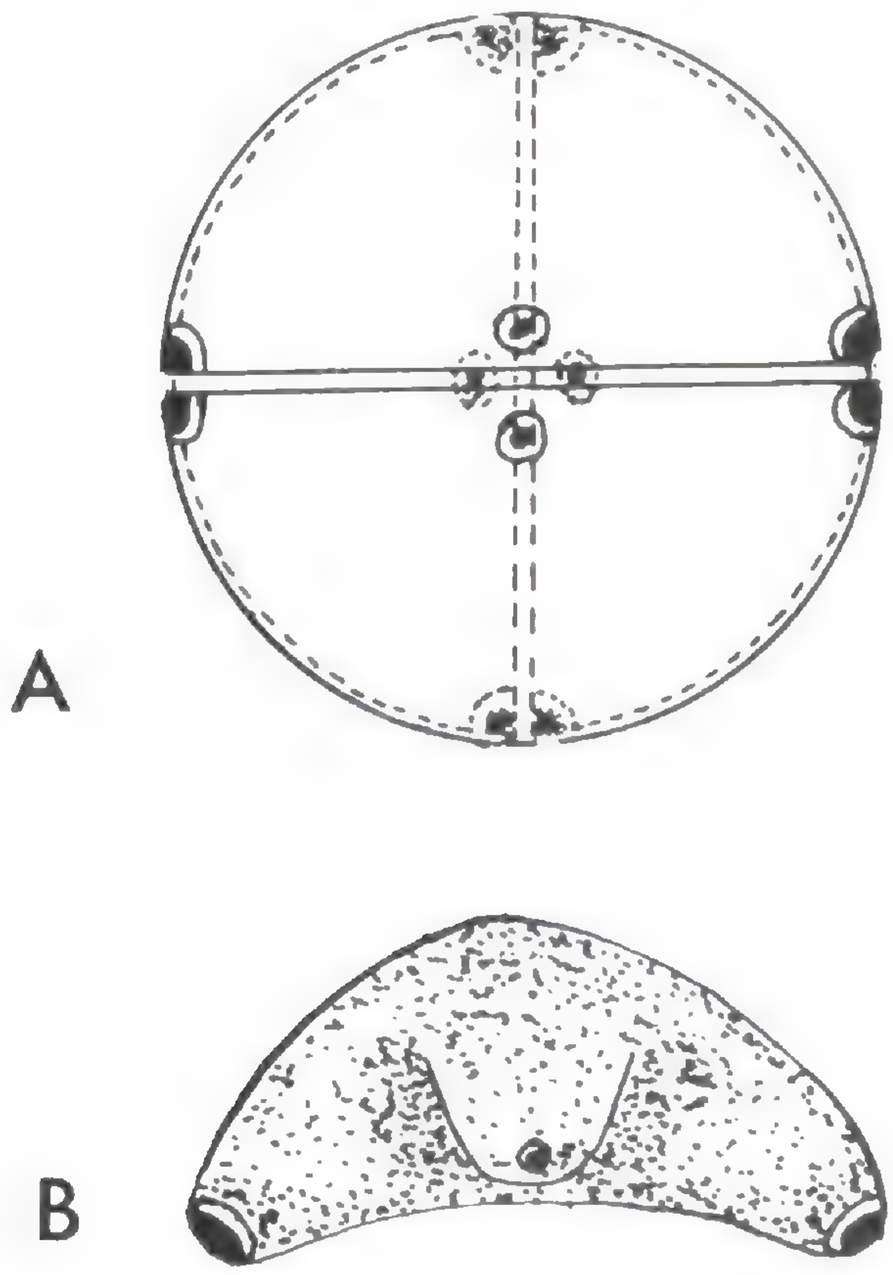

FIGURE 1.—Schematic drawings after photomicrographs of *Voyria clavata*, × 1,500. — A. Tetrad arrangement with 12 pores. — B. Single grain in lateral view, pore seen in face view smaller in size.

Philips EM-200 electron microscope. Acetolyzed, gold-coated pollen of *Voyria clavata* was examined with a Stereoscan Mk IIa scanning reflection electron microscope, at the Swedish Geological Survey, Stockholm.

RESULTS

Surface morphology was observed by light microscopy and occasionally by scanning electron microscopy, and fine structural characters were analyzed by transmission electron microscopy. Descriptions of surface morphology follow Erdtman (1943, 1952, 1966). Electron micrographs of thin sections are interpreted on the basis of exine stainability, and the terminology of Faegri (1956) is used. Accordingly the ektexine corresponds to sexine and nexine 1, and nexine 2 is equivalent to endexine.

Cotylanthera Blume. Fig. 2–3.

Pollen grains radially symmetrical, isopolar, oblate spheroidal to prolate (-perprolate), outline oval or rhomboid in lateral view, rounded-triangular and trilobate in polar view; 11–15 × 5–13μ; tricolporate, colpi comparatively wide, slightly constricted at equator, ora traceable in side view only, diameter of apocolpia 4–7μ; exine ca. 0.5μ thick, sexine appears to be as thick as nexine, smooth to granulate (LO-pattern), baculate.

Specimens examined: *Cotylanthera tenuis* Blume.—NEW GUINEA: Demta near Hollandia *BW 4121* (L); Island of Japen, Samberi, *Aët & Idjan 151* (L). SUMATRA: Korthals, *L. 909-57-418* (L). PHILIPPINES: Rizal, Luzon, *Loher 14701* (UPS).

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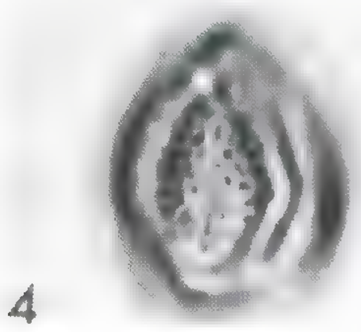

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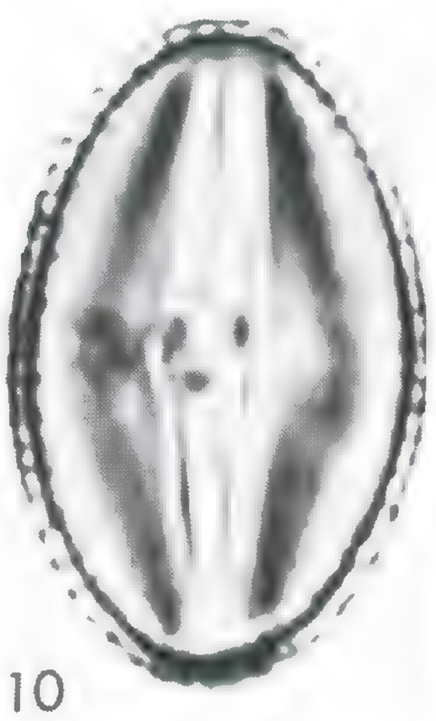

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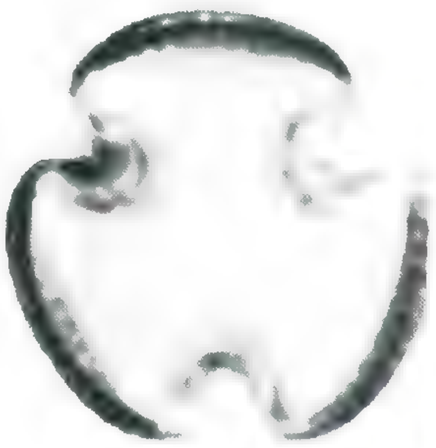

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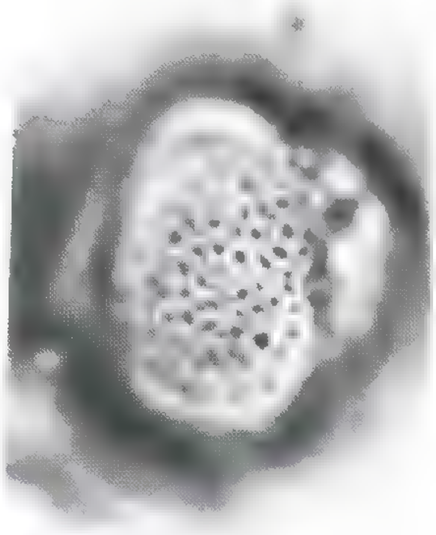

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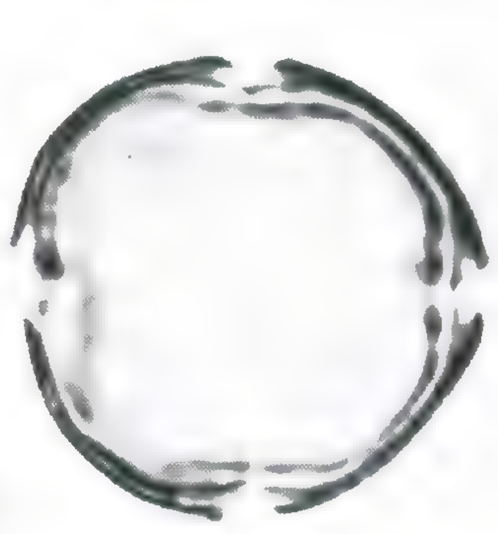

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Intraspecific variation. One specimen (*Loher 14701*) differs by having extremely prolate (perprolate) pollen grains which are comparatively narrow in lateral view.

Fine structure (*Fig. 49–50*). The endexine is sharply differentiated from the ektexine by electron density. The foot layer is thicker than the endexine in mesocolpia but highly reduced or absent at the colpi; bacules are short and broad.

Bartonia Mühl. *ex* Willd. Fig. 4–7.

Pollen grains radially symmetrical, isopolar, oblate spheroidal to prolate, outline oval or rhomboid in lateral view, rounded-triangular and trilobate in polar view; 11–19 × 10–15μ; tricolporate, colpi ± constricted at equator, ora small, ca. 1 × 1μ, or traceable in side view only, diameter of apocolpia 5–8μ; exine 1μ thick, sexine as thick as nexine or thicker, reticulate or with OL-pattern, less often striato-reticulate, reticulum delicate, lumina ca. 0.5μ in diameter (rarely up to 1μ), muri ca. 0.5μ wide, baculate.

Specimens examined: *Bartonia paniculata* (Michx.) Mühl. subsp. *paniculata*.—Nova Scotia: Lower Argyle, *Fernald, Bissell, Graves, Long & Linder 22288* (S); subsp. *iodandra* (Robins) Gillett. Nova Scotia: Île Madame, Arichat, *Rousseau 35563* (S).

Bartonia verna (Michx.) Mühl.—Florida: Riverview, *Blanton 6927* (S); 3 mi. W of Bithlo, *Moldenke 205* (S); Braidentown, *Tracy 7540* (S).

Bartonia virginica (L.) BSP.—Nova Scotia: Louis Lake, Port Joli, *Fernald, Long & Linder 22295* (S). Maine: *s. loc., Chickering*, 1875 (US). Massachusetts: Pelham, Mt. Lincoln, *Seymor 3789* (MASS); Amherst, *Torrey*, 1945 (MASS). New Jersey: Along Maurice River, W of Vineland, *Adams 977* (S).

Interspecific variation. *Bartonia paniculata* has pollen grains with a very fine reticulum or OL-pattern (lumina less than 0.5μ in diameter) and closely spaced bacules as compared with *B. verna* and *B. virginica* which have a coarser reticulum (lumina up to 1μ) and less closely spaced bacules.

Fine structure (*Fig. 43–45*). Fine structure similar to *Cotylanthera;* the upper surfaces of bacules are expanded and fused with adjacent bacules to form a reticulate to striato-reticulate pattern.

Obolaria L. Fig. 8–13.

Pollen grains radially symmetrical, isopolar, spheroidal to prolate, outline oval or rhomboid in lateral view, rounded triangular and trilobate in polar view; 19–28 × 17–21μ; tricolporate, colpi distinctly constricted at equator, ora traceable in side view only, diameter of apocolpia 6–8μ; exine 2μ thick, sexine as

←

Figures 2–18.—Pollen of saprophytic Gentianaceae, × 1,500. — 2–3. *Cotylanthera tenuis*.—2. Finely granulate sexine (LO-pattern).—3. Almost optical cross-section. — 4–7. *Bartonia paniculata* subsp. *paniculata*.—4. Finely reticulate sexine (OL-pattern).—5. Optical cross-section.—6. Colpus with small os in face view.—7. Polar view, optical cross-section. — 8–13. *Obolaria virginica*.—8. Reticulate sexine, at higher focal plane.—9. Reticulate sexine, at lower focal plane.—10. Optical cross-section.—11. Constricted colpus in face view.—12. Near optical cross-section, two colpi with ora in lateral view.—13. Polar view, optical cross-section. — 14–18. *Voyriella parviflora*.—14. Finely reticulate sexine (OL-pattern).—15. Optical cross-section.—16. Colpus with distinct os having lateral extensions.—17. Polar view of tetracolporate grain, sexine reticulate.—18. Polar view, optical cross-section.

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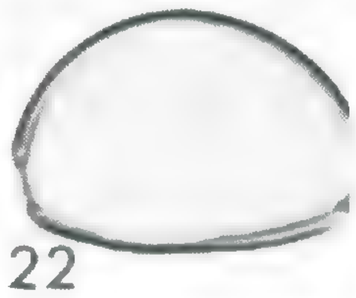
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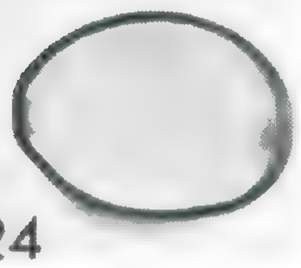
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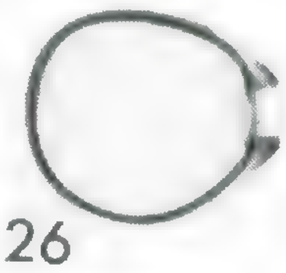
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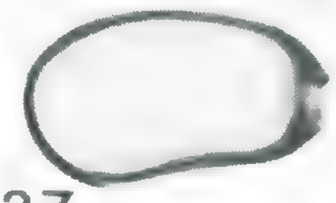
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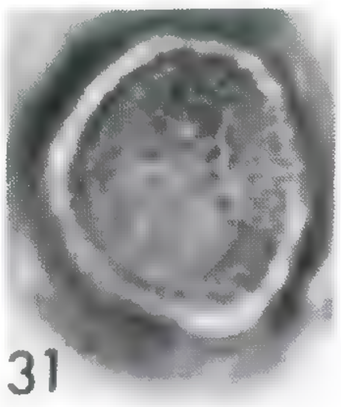
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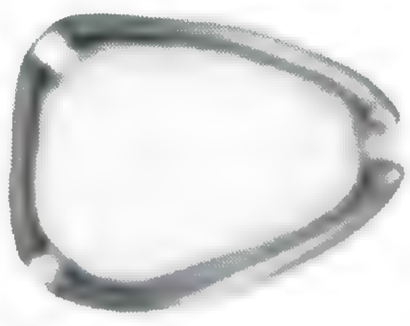
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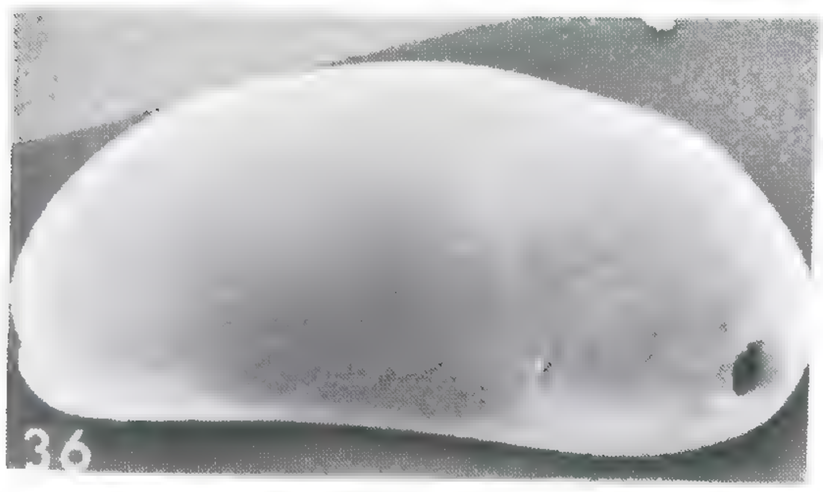
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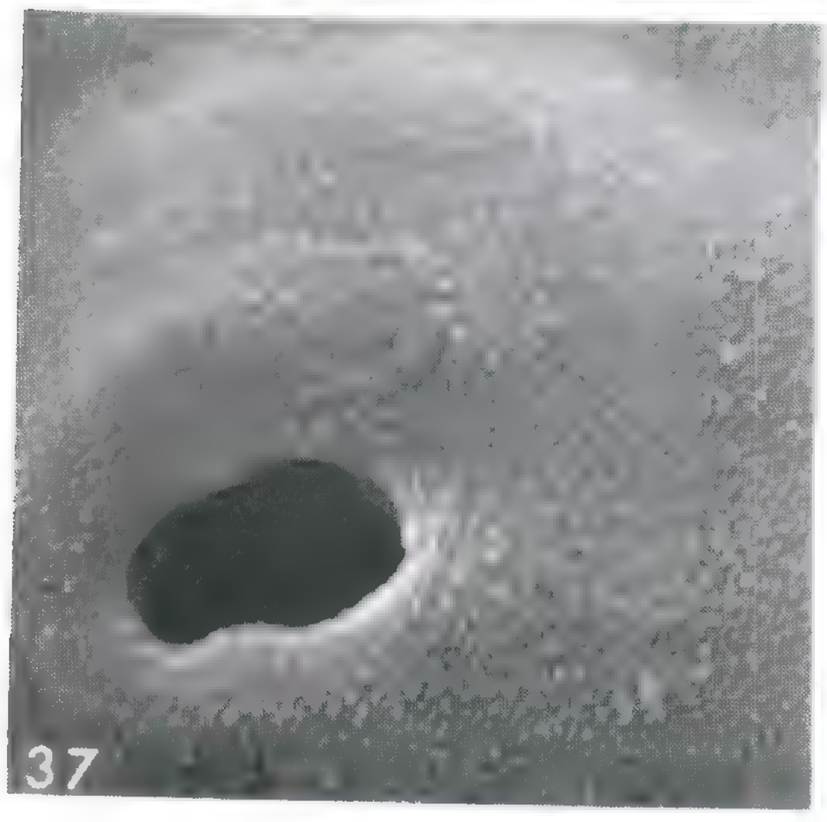
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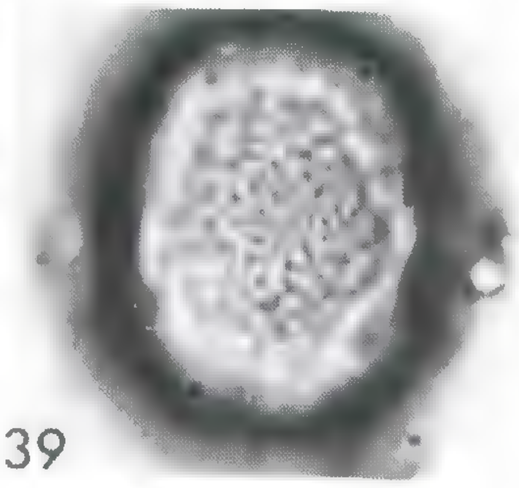
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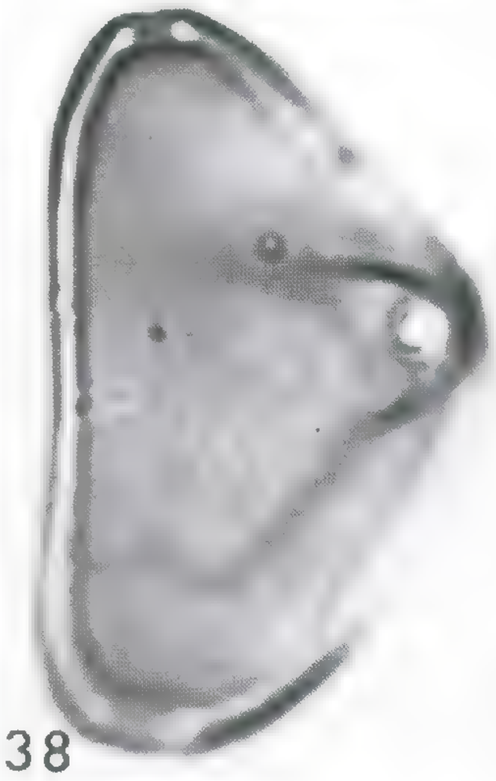
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thick as nexine or thicker, reticulate, lumina ca. 0.5–1.5μ in diameter, muri ca. 0.5μ wide, baculate.

Specimens examined: *Obolaria virginica* L.—WASHINGTON, D.C.: *Lenander,* 1926 (S). INDIANA: Posey Co., *Deam* 27035 (NY, US). NORTH CAROLINA: SW of Hillsboro, *Ahles & Haesloop* 53200 (S).

Fine structure (Fig. 46–48). Fine structure similar to *Bartonia.*

Voyriella (Miq.) Miq. Fig. 14–18.

Pollen grains radially symmetrical, isopolar, suboblate to prolate spheroidal, outline circular to oval in lateral view, ± circular and tri- to tetralobate in polar view; 13–20 × 14–20μ; tri- to tetracolporate, colpi meridional, or when four obliquely converging into pairs, ora usually lalongate (ca. 2 × 6μ) with lateral extensions, diameter of apocolpia 7–8μ; exine 1–1.5μ thick, sexine as thick as nexine, or thicker, reticulate or with OL-pattern, lumina ca. 0.5(–1.0)μ in diameter, muri ca. 0.5μ wide, baculate.

Specimens examined: *Voyriella oxycarpha* Sandw.—SURINAM: Maratakka River, Snake Creek, *L. B. B. 10767* (U).

Voyriella parviflora (Miq.) Miq.—SURINAM: Brokopondo district, *Donselaar 2469, 3165* (both U); Nassau Mountains, *Lanjouw & Lindeman 2229* (NY, U); Kabel, *Lindeman 4482* (U); Moengo, *Lindeman 5768* (U).

Fine structure (Fig. 51–52). Endexine is approximately the same thickness as foot layer. Short bacules support a thick, slightly perforate tectum. Similar to *Bartonia.*

FIGURES 19–42.—Pollen of saprophytic Gentianaceae, 19–35, 38–42, × 1,500; 36, × 2,100; 37, × 6,200.—19–22. *Leiphaimos corymbosus* (19–21, *Lanjouw & Lindeman 2396;* 22, *Sandwith 1065*).—19. Radially symmetrical, isopolar grain with one of three pores in face view.—20. Optical cross-section.—21. Polar view, optical cross-section.—22. Bilateral, heteropolar grain, depressed ovate, diporate.—23. *Leiphaimos spruceanus,* radially symmetrical, isopolar, diporate grain in optical cross-section, pores with prominent annular thickening.—24–25. *Leiphaimos aphyllus.*—24. Bilateral, heteropolar and diporate grain in polar view.—25. Same, convexo-plane, pores with annular thickening.—26 27. *Leiphaimos flavescens.*—26. Monoporate grain in lateral (?) view, pore with prominent annulus.—27. Monoporate, elongated grain in lateral (?) view, pore with annular thickening. — 28–29. *Leiphaimos aurantiacus.*—28. Bilateral, heteropolar, diporate grain in polar view.—29. Same, convexo-plane, pores without annular thickening. — 30. *Leiphaimos tenuiflorus,* bilateral, heteropolar, diporate grain, convexo concave. — 31 35. *Leiphaimos calycinus* (31–33, *Versteeg 154;* 34–35, *Donselaar 2463*).—31. Radially symmetrical, isopolar, diporate grain, sexine surface with coarse texture.—32. Same, one pore with annular thickening in face view.—33. Same in optical cross-section, prominent annular thickening.—34. Bilateral, heteropolar, triporate grain in polar view.—35. Same, diporate grain in polar view. — 36–38. *Voyria clavata* (36 37, Brownsberg, *Stahel s.n.;* 38, *Donselaar 1982*).—36. Bilateral, heteropolar, diporate grain, convexo-concave (reniform), scanning electron micrograph.—37. Pore with slightly protruding rim and finely granular sexine surface at higher magnification, scanning electron micrograph. — 38. Triporate grain in slightly oblique position, lateral view, convexo-concave. — 39–42. *Voyria rosea* (39–40, *B.W. 941;* 41–42, *Florschütz & Maas 2834*).—39. Radially symmetrical, isopolar, diporate grain, sexine surface with coarse texture.—40. Same, optical cross-section, pores with annular thickening.—41. Bilateral, heteropolar, triporate grain in polar view.—42. Bilateral, heteropolar, diporate grain, convexo-concave.

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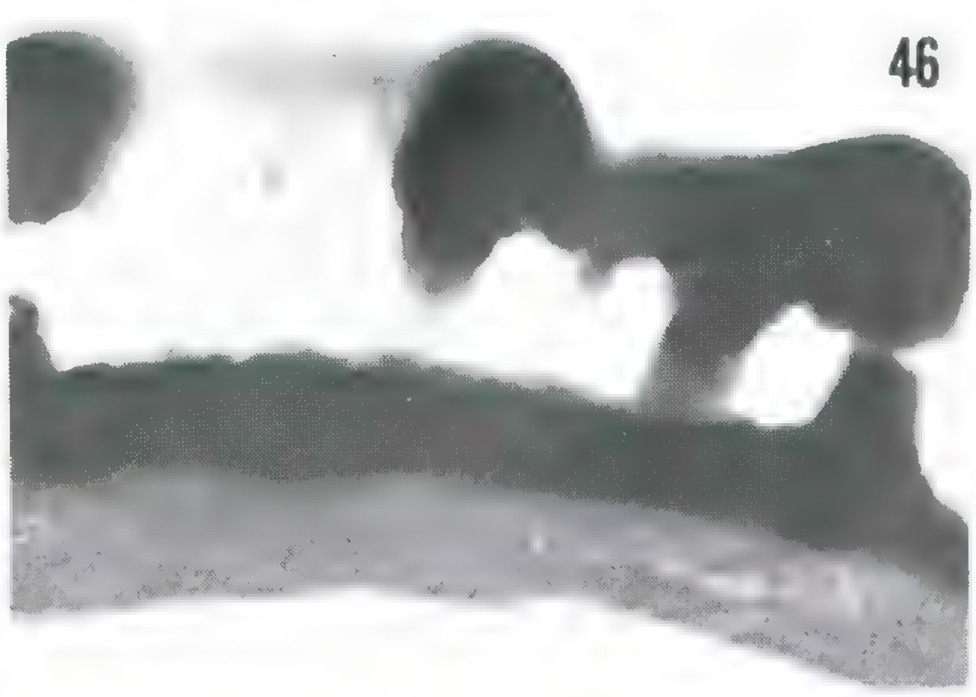
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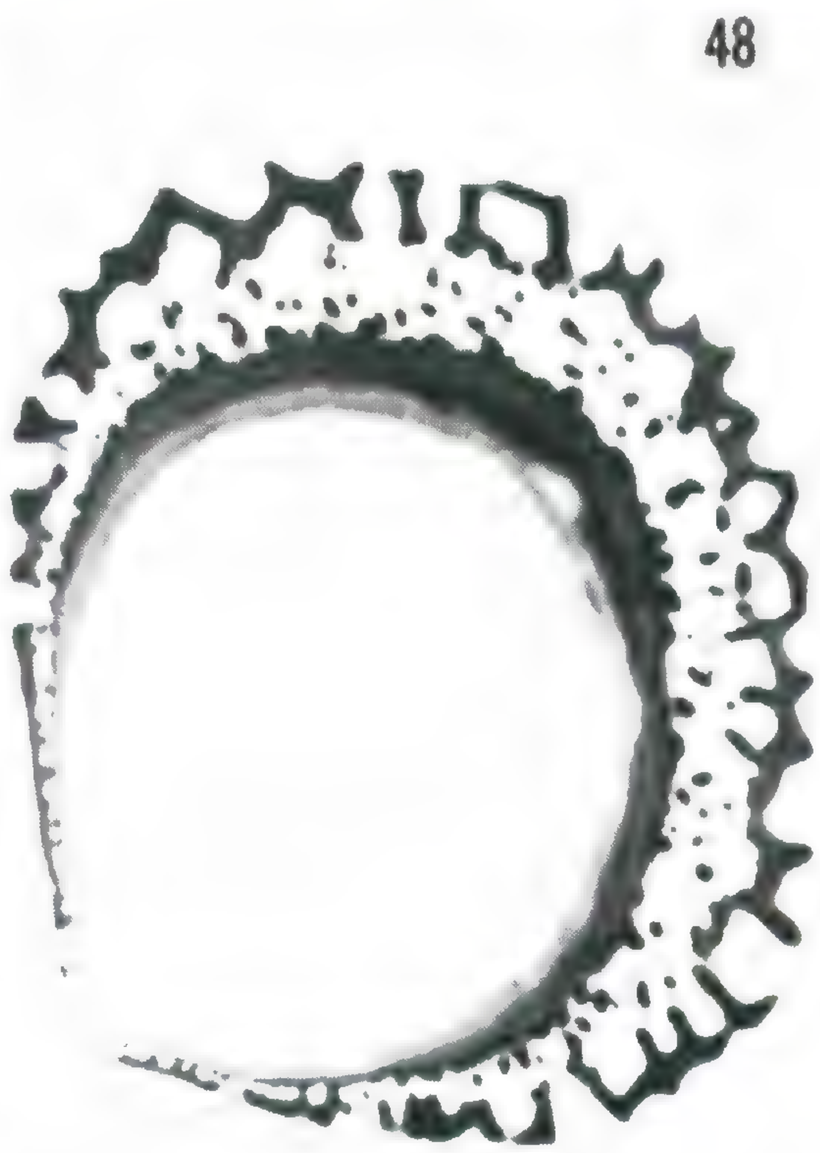
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Leiphaimos Cham. & Schlechtd. Fig. 19–35.

Pollen grains bilateral, heteropolar, reniform, semi-ovoidal to unsymmetrically biconvex, or radially symmetrical, isopolar, oblate to spheroidal, or irregular, outline in lateral view convexo-concave,[5] convexo-plane[5] to depressed ovate, or ± circular, in polar view circular to oval, or irregular; 7–13 × 11–24 × 8–15μ ($P \times E_1 \times E_2$) or 9–22 × 11–18μ ($P \times E$) or diameter 11–20μ; one to six-porate, pore diameter 1–3μ, pore margin reinforced by an annular thickening ca. 0.5–1μ wide, 1–2μ high, consisting of thickened sexine or nexine or both, annulus occasionally absent; exine ca. 0.5–1μ thick, at the apertures up to 2μ thick, stratification obscure although the exine appears divided into sexine and nexine at the apertures, sexine smooth or rough (scabrous), non-baculate.

The pollen of *Leiphaimos* has been grouped into a number of types which are not sharply defined from each other. The grouping is to be considered an attempt to assort the variation observed within the genus.

1. *Leiphaimos parasiticus*-type. Pollen grains radially symmetrical (rarely bilateral), isopolar, suboblate to spheroidal or irregular; 3- to 4-porate, pores of varying size, diameter 1–2μ, annular thickening usually relatively faint; sexine surface smooth. Fig. 19–22.

Specimens examined: *Leiphaimos albus* Standl.—PANAMA: Barro Colorado Island, *Dodge,* 1934 (MO); Colón, *Dodge, Steyermark & Allen 16927* (MO).

Leiphaimos corymbosus (Splitg.) Gilg.—GUYANA: Mazaruni Station, *Sandwith 1065* (U). SURINAM: Nassau Mountains, *Cowan & Lindeman 39184* (NY); *Lanjouw & Lindeman 2396* (U); Maratakka River, Snake Creek, *Maas 3279* (U); Brokopondo district, *Donselaar 1688* (U).

Leiphaimos montanus Jonk.—SURINAM: Wilhelmina Range, *B.W. 6982 p.p.* (type, U).

Leiphaimos parasiticus Schlechtd. & Cham. —MEXICO: Chiapas, *Dressler 1410* (US). CUBA: Pinar del Río, *Ekman 17333* (S); Oriente, *Ekman 2085* (S). HAITI: Mountains Terre-Nueve, *Ekman 5036* (S). BRAZIL: Pernambuco, *Pickel 4011* (S).

Inter- and intraspecific variation. One specimen of *L. corymbosus (Sandwith 1065)* has bilateral, heteropolar pollen grains instead of the generally radially symmetrical ones and is better referred to the *Leiphaimos tenuiflorus*-type of pollen. Another collection *(Maas 3279)* has curved or more or less irregular pollen grains with a large number of pores and a scabrous sexine surface. In *L. parasiticus* itself there are specimens that tend to have slightly curved pollen grains.

Fine structure (Fig. 56–57). Observations are for *L. parasiticus.* Endexine is considerably thicker than ektexine; at aperture margins endexine is prominently thickened. Upper surface of endexine (or foot layer) is slightly lamellate. Foot

[5] Outline in lateral view according to Straka, 1964. (*Cf.* also *Voyria.*)

FIGURES 43–48.—Electronmicrographs of pollen of saprophytic Gentianaceae. — 43–45. *Bartonia paniculata* (Michx.) Mühl. subsp. *paniculata.*—43. Near median section, × 7,200. —44. Oblique view emphasizing reticulate nature of sexine, × 11,400.—45. View through apocolpium, × 39,200. — 46–48. *Obolaria virginica* L.—46. View through apocolpium, × 34,000. Note similarity to Fig. 45.—47. Near median section, × 7,200.—48. Oblique view, × 11,000. Note similarity to Fig. 44.

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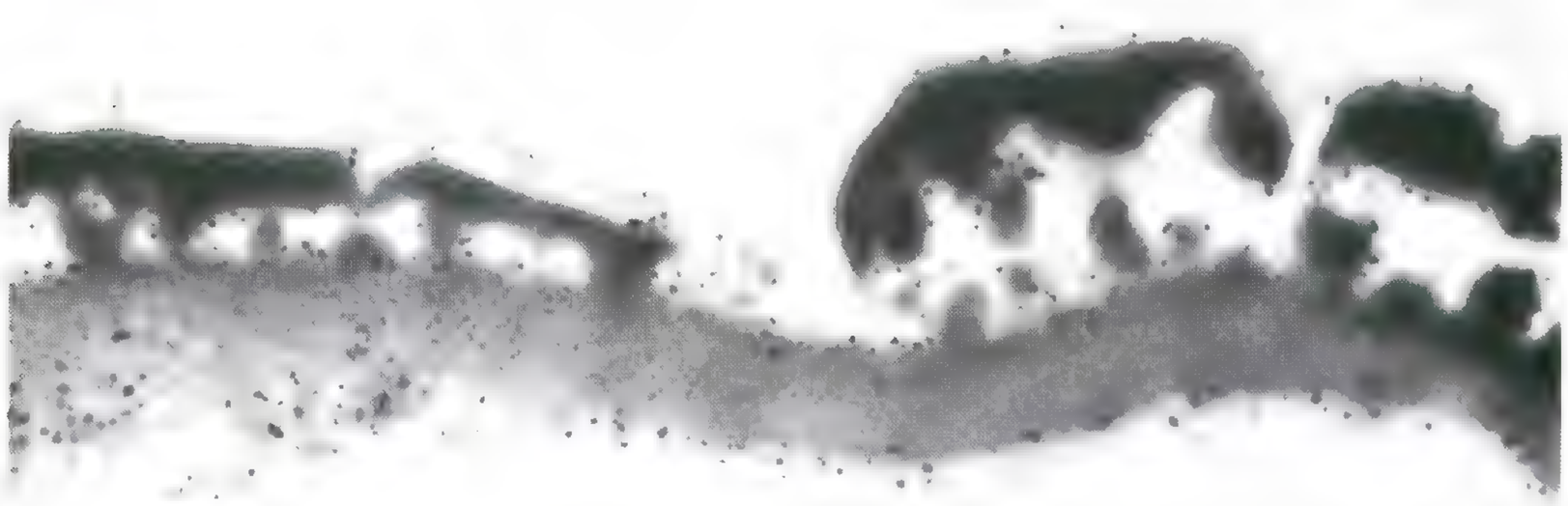
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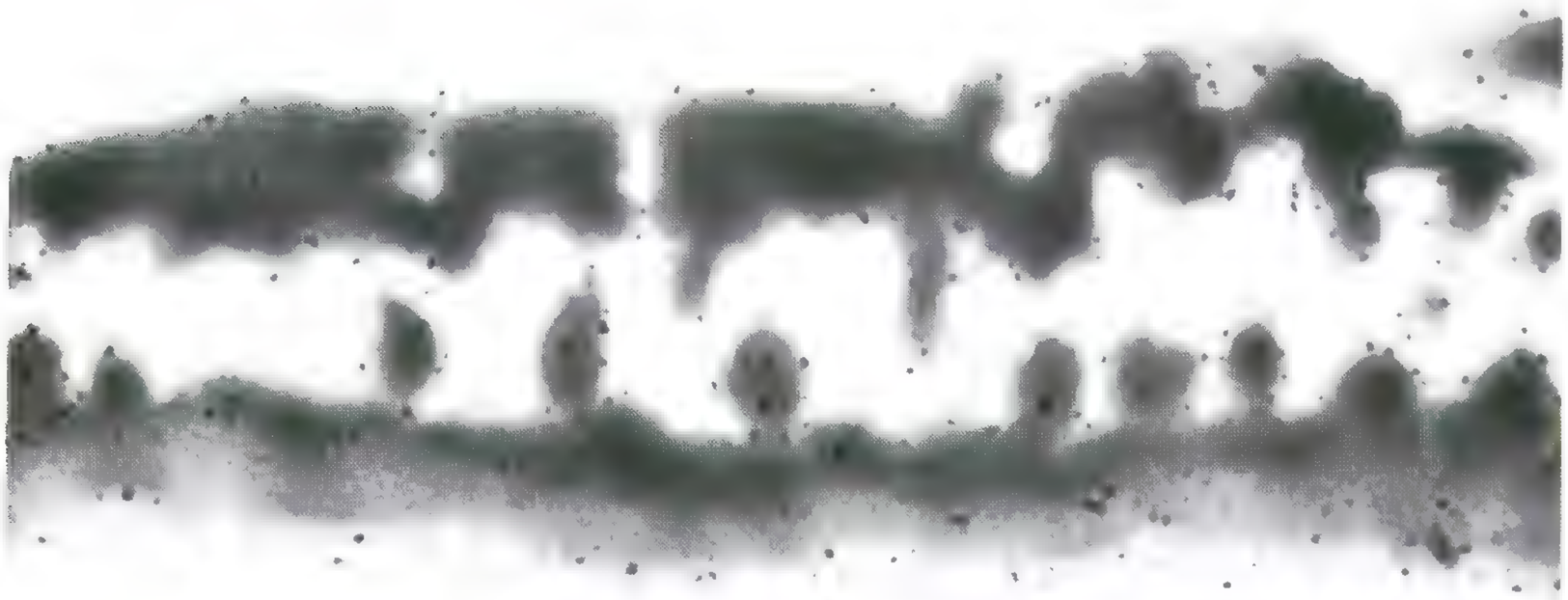
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layer reduced and supports minute and fragile bacules. A markedly thickened tectum, which is slightly perforate, extends over the bacules.

2. *L. spruceanus*-type. Pollen grains radially symmetrical, isopolar, ± spheroidal 2- to 6-porate, pores 1–2μ in diameter, with a prominent annular thickening, ca. 0.5–1μ wide, 1μ high; sexine smooth or scabrous. Fig. 23, 31–33.

Specimens examined: *Leiphaimos calycinus* (Griseb.) Miq.—SURINAM: Nickerie River, *L. B. B. 11045* (U); Maratakka River, Snake Creek, *Maas* 3272 (U); Gonini River, *Versteeg 154* (U). The other collections examined resemble *e.g., Voyria caerulea.*

Leiphaimos spruceanus (Benth.) Gilg.—SURINAM: Brownsweg, *Donselaar 3000* (U); Brokopondo district, *Donselaar 3153* (U); without locality, *Stahel 402* (U).

Voyria rosea p.p. (Fig. 39–40) has the same type of pollen as *L. spruceanus.*

Intraspecific variation. *L. calycinus* has pollen of the *Leiphaimos spruceanus*-type, but some specimens *(Donselaar 2463, 3045)* resemble those of *Voyria caerulea.*

3. *L. aphyllus*-type. Pollen grains bilateral, heteropolar or rounded to irregular in shape; 1- to 2-porate, pores 1–2μ in diameter, with a prominent annulus, ca. 0.5μ wide, 1μ or more high; exine ca. 0.5(–1.0)μ thick, sexine smooth. Fig. 24–27.

Specimens examined: *Leiphaimos aphyllus* (Jacq.) Gilg. CUBA: Sierra Maestra, *Ekman 5353* (S). HAITI: Port Margot, *Ekman 2820* (S); Massif du Nord, *Ekman 4837* (NY). SURINAM: Without locality, *Stahel 403* (U); Donderkreek-Wayambo River, *Stahel 1915* (U); Brownsweg, *Wessels-Boer 600* (U).

Leiphaimos flavescens (Griseb.) Gilg.—SURINAM: Coppename district, *Florschütz & Maas 2639* (U).

Voyria primuloides cited by Raynal (1967) has a similar type of pollen.

4. *L. tenuiflorus*-type. Pollen grains bilateral, heteropolar or irregular; 1- to 2-porate, pores 2–4μ in diameter, devoid of annular thickening, pore margins often folded outwards; exine 0.5–1μ thick, sexine smooth. Fig. 28–30.

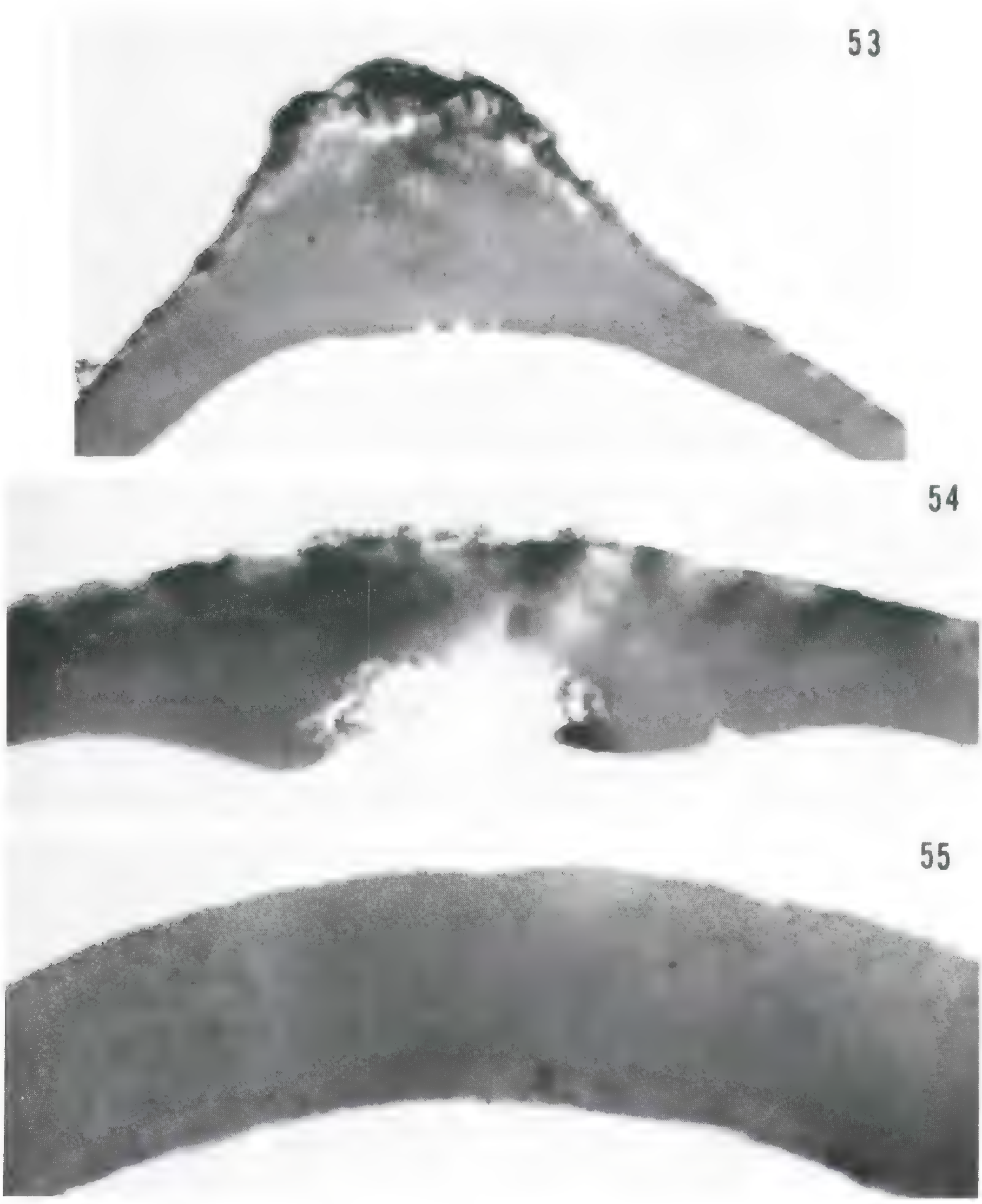
Specimens examined: *Leiphaimos aurantiacus* (Splitg.) Miq. SURINAM: Maratakka River, Snake Creek, *L. B. B. 10768* (U); Jande Creek near Kabel Station, *Lindeman 4430* (U). GUYANA: Mazaruni Station, *Davis*, 1937 (S, U). BRAZIL: Maracassume, Mato do Caxoeira, *Moses 57* (U).

Leiphaimos leucanthus (Miq.) Gilg.—SURINAM: Commevijne River, Tempatikreek, *Focke 1253* (U).

Leiphaimos tenellus (Hook.) Miq.—PANAMA: Without locality, *Dodge, Steyermark & Allen 16926* (U); Darien, Puerto St. Dorotea, *Duyer 2284* (MO). COLOMBIA: La Jagua, Magdalena Valley, *Allen 581* (U).

Leiphaimos tenuiflorus (Griseb.) Miq.—SURINAM: Linker-Coppename River, *Florschütz & Maas 3156* (U); Nassau Mountains, *Lanjouw & Lindeman 2722* (U).

FIGURES 49–52.—Electronmicrographs of pollen of saprophytic Gentianaceae. — 49–50. *Cotylanthera tenuis* Bl.—49. View across colpus showing reduction of ektexine and thick endexine. × 13,050.—50. View along apocolpium, × 58,800. Note lamellae near upper surface of endexine (arrow). — 51–52. *Voyriella parviflora* (Miq.) Miq.—51. View near margin of colpus, × 26,000. Black dots are OsO_4 precipitate.—52. View along apocolpium, × 26,000. Black dots are OsO_4 precipitate.



Figures 53–55.—Electronmicrographs of *Voyria rosea* Aubl.—53. View oblique to aperture margin, × 22,750. Note thin, electron dense cap over otherwise homogeneous exine. —54. View oblique to pore, × 50,400.—55. View along apoporium, × 97,000. Note that electron dense cap is not evident.

Interspecific variation. *L. aurantiacus* has larger grains than the other species referred to of this type. The pore margins are distinctly folded outwards, the pollen wall appears to be thicker, and the shape more stable than in the other species.

Fine structure (Fig. 58–62). Exine stratification is difficult to interpret. The exine appears to consist of a single layer; however, fine lamellae are present on the upper part of the exine. These lamellae are most clearly observed in

unacetolyzed material. An intine which approaches the exine in thickness is visible in the unacetolyzed pollen. Numerous dense inclusions are present within the intine.

Voyria Aubl. Fig. 36–42.

Pollen grains bilateral, heteropolar, reniform, semi-ovoidal to unsymmetrically biconvex or radially symmetrical, isopolar, ± spheroidal or irregular, outline in lateral view convexo-concave, convexo-plane to depressed ovate, or ± circular, in polar view circular to oval, or irregular; 9–20 × 17–31 × 10–18μ (P × E_1 × E_2) or 10–18 × 15–18μ (P × E) or diameter 10–15μ; one- to six-porate, pore diameter 2–3μ, pore margin reinforced by an annular thickening ca. 0.5μ wide and 0.5–1μ high, consisting of thickened sexine or nexine or both; exine 0.5–1μ thick, at the apertures up to 2μ thick, stratification obscure although the exine appears divided into sexine and nexine at the apetures, sexine smooth or rough (*cf.* Fig. 36), non-baculate.

The pollen grains of *Voyria* are basically the same as those of *Leiphaimos*.

Specimens examined: *Voyria clavata* Splitg.—SURINAM: Brokopondo district, *Donselaar 1982* (U); Brownsberg, *Stahel* (U); without locality, *Florschütz 1828;* without locality, *Stahel* (U).

Voyria caerulea Aubl.—SURINAM: Emma Keten, *Jonker & Daniels 732* (U); Saramacca River, *Maguire 24130* (U); Rechter-Coppename River, *Wessels-Boer 1391* (U).

Voyria rosea Aubl.—SURINAM: Maratakka River, *B. W. 941* (U); Bakhuisgebirge, *Florschütz & Maas 2834* (U); Nickerie River, *L. B. B. 10913* (U). GUYANA: Kaieteur Plateau, *Maguire & Fanshawe 23140* (U).

Intraspecific variation. One collection of *Voyria rosea (B.W. 941)* has radially symmetrical, 2-porate, pollen grains (=*Leiphaimos spruceanus*-type) while the other specimens have grains of the elongated, curved type (*cf. Leiphaimos calycinus p.p.*, Fig. 34–35) or are irregular in shape.

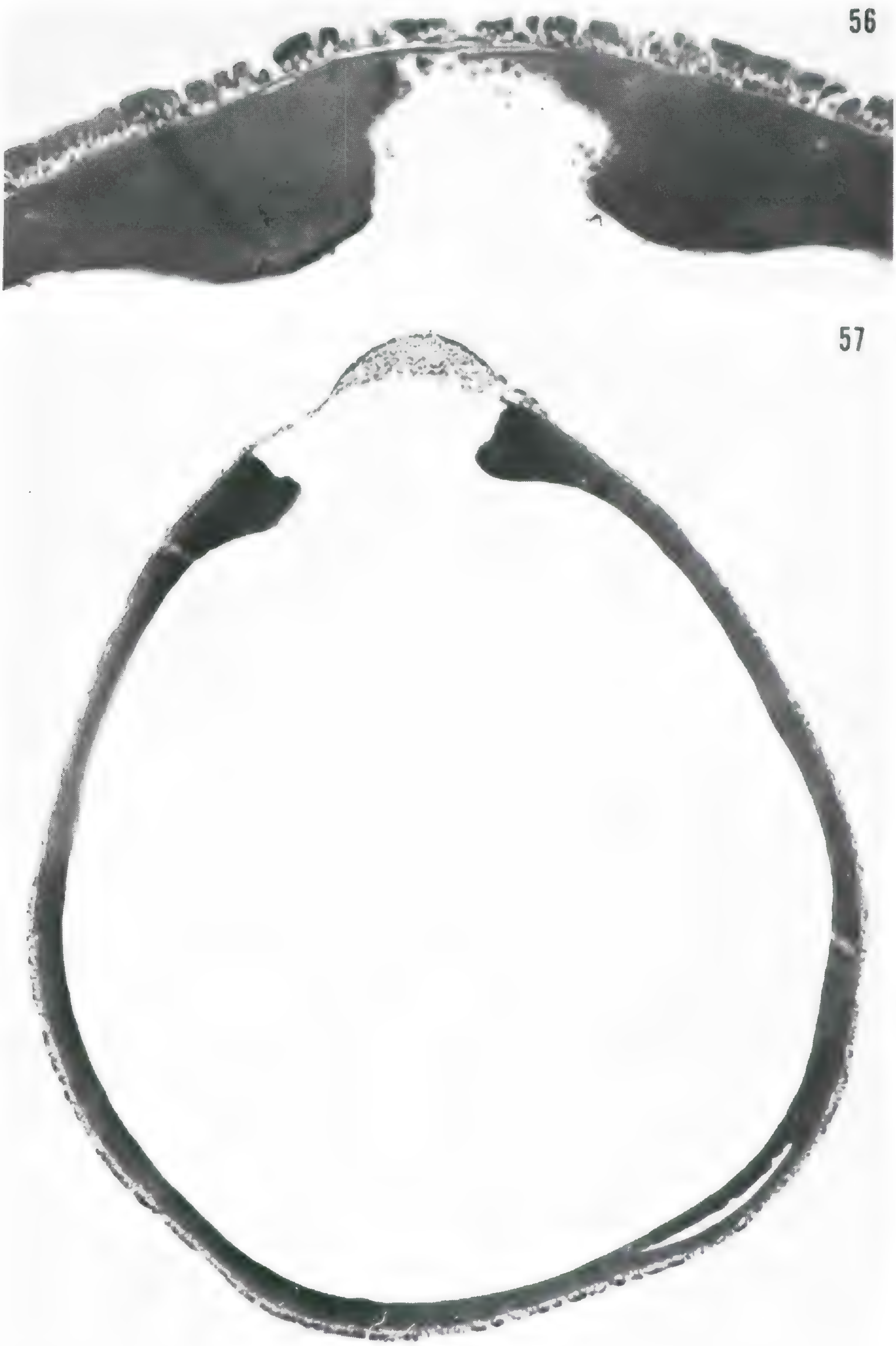
Fine structure (Fig. 53–55). Exine is thin, and differentiation into ektexine and endexine is extremely difficult. Ektexine is most clearly observed at pores and consists of an electron dense band. In other sections an ektexine is not recognized.

Discussion of Surface Morphology

Polarity. Previous interpretations of polarity in *Voyria* do not agree with our study. While the pores have been considered polar (Gilg, 1895; Köhler, 1905; Oehler, 1927), it seems more likely that they are equatorial (Fig. 1).

In one collection of *Voyria clavata* some of the pollen grains are united in tetrads. The grains are arranged in pairs and each pair is in a different plane. The polar axes of each pair cross those of the other pair at right angles or nearly so (Fig. 1A). The pores meet in pairs at six places or at four places. A similar tetrad arrangement has been reported for other families, *e.g.* Balsaminaceae, Saxifragaceae, Tropaeolaceae, (Huynh, 1968, Fig. 37, 39, 41, 47–49).

In one specimen of *Leiphaimos spruceanus (Donselaar 3153)* square, rhomboidal and linear tetrads are found. Isopolar grains occur in all genera examined, but in *Voyria* and *Leiphaimos* they are prevailingly heteropolar.



Figures 56 57.—Electronmicrographs of *Leiphaimos parasiticus* Schlechdt. & Cham.—56. View oblique to pore, × 29,300. Note highly reduced ektexine with thick tectum and foot layer composed of fine lamellae.—57. View through entire pollen grain, × 9,900. Note granular appearance of endexine under pore.

Symmetry and Shape. Radially symmetrical grains occur in all taxa, although *Voyria* and *Leiphaimos* have predominantly bilateral, elongated, more or less curved pollen. In the Gentianaceae the latter type of pollen is found exclusively in these two genera, but it has also been reported in Proteaceae (Erdtman, 1952; Smith, 1968), Tropaeolaceae and Saxifragaceae (Huynh, 1968). Since the rounded tri- or more -porate grains appear to be radially symmetrical with an equatorial arrangement of pores, it seems that those of elongated grains are also in an equatorial plane. Consequently one might consider the curved pollen of *Leiphaimos parasiticus* or *L. corymbosus* as being derived from radially symmetrical ones that occur within or between single collections. Oehler (1927) considered young, one-celled pollen of *Voyria* to be spheroidal and older pollen to be curved, possibly due to uneven growth of the surface. Oehler's conclusion seems plausible when considering the variable outlines of pollen grains. In accordance with Oehler, younger grains of *Cotylanthera* are spheroidal; older grains more or less triangular.

Size. Most genera examined have relatively small pollen grains (longest axis less than 20μ). *Obolaria* has relatively large grains, and *Voyria* has larger grains on the average than *Leiphaimos*.

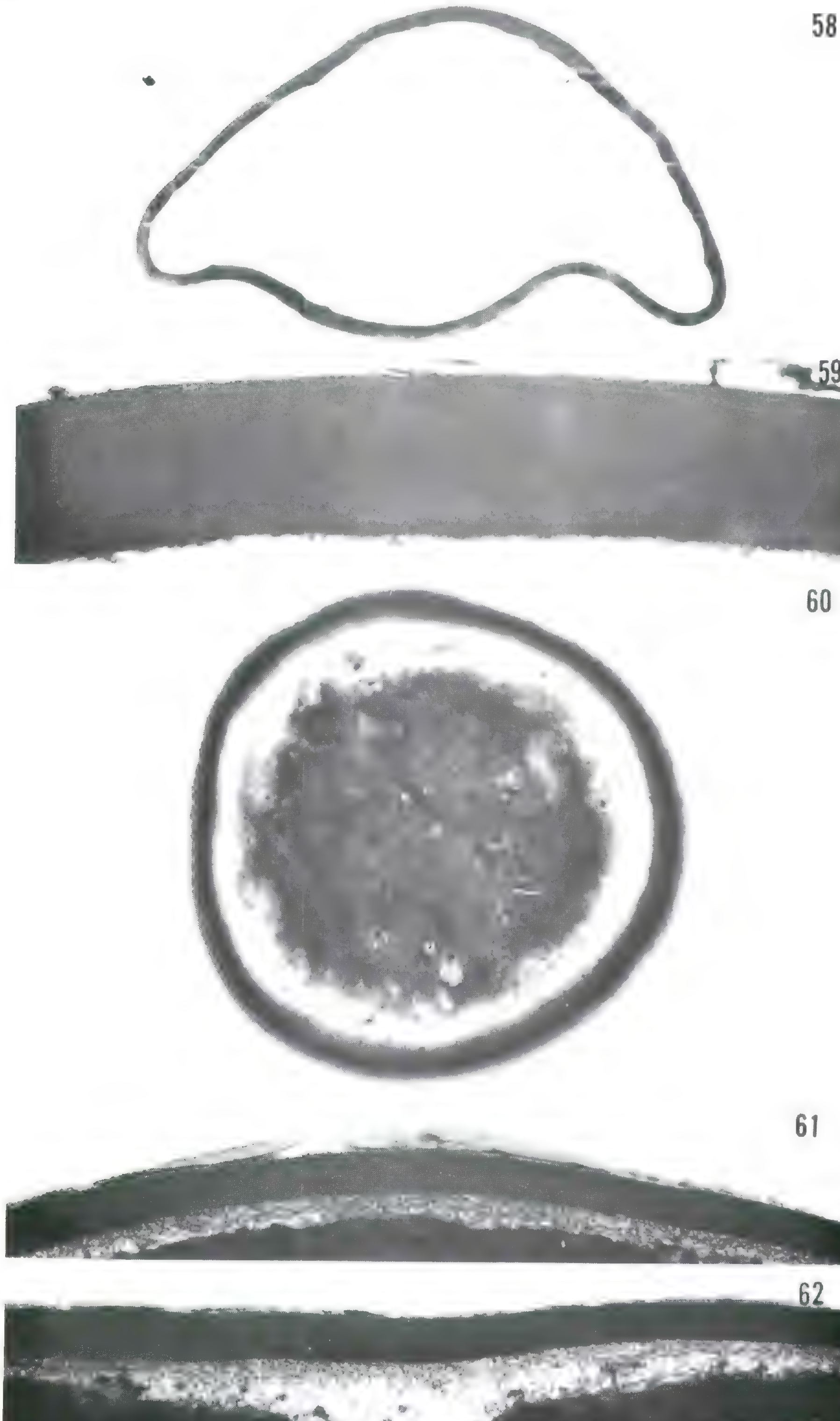
Apertures. The colpi of pollen of *Bartonia* and *Obolaria* are usually constricted at the equator (*cf.* Iverson & Troels-Smith, 1950, Pl. 15, 3d, 3e). The number of apertures varies considerably. Porate grains occur in *Leiphaimos* and *Voyria*. According to Gilg (1895) *Leiphaimos* has ovoidal pollen with one apical pore, while *Voyria* has "Einzelpollen schwach wurstförmig gebogen" (pollen slightly curved, sausage-like) with two apical pores. We have found that neither the number of apertures nor the pollen shape are stable enough characters to differentiate the two genera. It is not unusual for one of the pores to be smaller than the others, an observation in agreement with Erdtman (1952). The reduction of pore size and number of pores suggests that the monoporate grains may be derived from polyporate (diporate) ones as exemplified by the monoporate and elongated pollen of *Leiphaimos flavescens* (Fig. 27).

The other genera studied, *Bartonia, Cotylanthera, Obolaria,* and *Voyriella,* all have three- (to four-) colporate pollen grains. The ora are usually indistinct except for *Voyriella* where they are sharply delimited and often provided with lateral extensions. The latter is a common feature in other groups of Gentianaceae (Nilsson, 1967).

Discussion of Fine Structure

Pollen fine structure of the saprophytic taxa shows a diversity in morphology. To an extent this diversity was consistent with the morphological differences noted by light microscopy. *Bartonia, Obolaria,* and *Cotylanthera* were practically indistinguishable with electron microscopy, and *Voyriella* was very similar to these genera.

Stratification in *Voyria rosea* was difficult to interpret. The exine appeared to be one layer except for a fine, electron dense band covering the outer surface (Fig. 53–54). This band was not always obvious (Fig. 55), and therefore exine


58
59
60
61
62

interpretation must be somewhat tentative. However, we feel that the band is real and probably is a highly reduced ektexine. We hope to do further work which will clarify this.

Fine structure of *Leiphaimos* indicated considerable interspecific variation. In *L. parasiticus* a reduced tectate ektexine was clearly observed, but in *L. aurantiacus* and *L. tenellus* the ektexine was not evident. Contrary to Gilg (1895) and Köhler (1905) we have found an intine in *L. tenellus* which substantiates some past interpretations for the genus (Oehler, 1927; Raynal, 1967). However, the intine of *L. tenellus* was considerably thicker than that described for *L. parasiticus* (Raynal, 1967). Although the electron microscopic sampling was limited, the fine structure of *Leiphaimos* is considered close to that of *Voyria rosea*.

Taxonomic Evaluation of the Pollen Morphological Data

Bentham and Hooker (1876) placed *Cotylanthera* in the tribe Exaceae together with *Exacum, Sebaea, Belmontia,* and *Tachiadenus*. They considered *Cotylanthera* closely allied to *Exacum* but differing by reduced leaves and anthers with one apical locule and pore. This staminal feature induced Gray (1868) to refer *Eophylon, i.e., Cotylanthera, to* Grisebach's subtribe Chironieae, but also influenced Baillon (1891) to reduce *Cotylanthera* to a section of *Exacum*. Gilg (1895) kept *Cotylanthera* as a genus in the Gentianeae-Exacinae, which was characterized by small pollen grains with a smooth exine surface, barely traceable furrows, and indistinguishable exine and intine. Köhler (1905) described the pollen of *Cotylanthera tenella* as triporate with a smooth exine.

In our study only *Cotylanthera tenuis* was available. The pollen morphology agrees with earlier interpretations of a smooth exine surface (Gilg, 1895; Köhler, 1905); however, a fine granulation was also evident. With the light microscope we have not been able to distinguish pores (ora) with certainty; with electron microscopy the ora were readily apparent.

We have not found any palynological evidence to suggest a close relationship between *Cotylanthera* and *Exacum*. In contrast to *Cotylanthera, Exacum* has striate to striato-reticulate pollen. The small pollen grains which characterize Gilg's subtribe Exacinae also occur in some genera of the Erythraeinae (*e.g., Bartonia, Schinziella, Curtia*).

Grisebach (1839, 1845) placed *Centaurella* (*i.e., Bartonia*) in the Swertieae near *Pleurogyne* (*i.e., Lomatogonium*). Bentham and Hooker (1876) also placed *Bartonia* and *Obolaria* (the latter genus was omitted by Grisebach) in the Swertieae, while Gilg (1895) placed them in the Gentianeae-Erythraeinae (charac-

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FIGURES 58–62.—Electronmicrographs of pollen of *Leiphaimos*. — 58–59. ***Leiphaimos aurantiacus*** **(Splitg.) Miq.—58. View through pollen, pores not included, × 6,300. Note similarity of exine to Fig. 55.—59. Homogeneous appearance of exine except for fine lamellae near upper surface, × 50,400. — 60–62. Unacetolyzed pollen of *Leiphaimos tenellus* (Hook.) Miq.—60. View through pollen, pore not included, × 26,000.—61. Fine lamellar band appearing to partially split from upper surface, × 73,500.—62. View oblique to pore, × 58,800. Note intine.**

terized by fairly large pollen grains with deep furrows and a smooth or granulated exine differentiated from the intine). Köhler (1905) described the pollen grains of *Bartonia verna* as reticulate with three furrows and three pores, while those of *B. tenella* (*B. virginica sensu* Gillett) had a smooth exine. Our investigation has shown a reticulate sexine for both species. The pollen of *Obolaria virginica* was described as "globosum, membrana tenuissima laevissima" (globose with a smooth and very thin wall) by Gray (1848) and as "oblong" with a "distinctly granulate exine" by Holm (1897). The latter author concluded from his morphological and anatomical studies that *O. virginica* was to be considered a connecting link between the autophytic and saprophytic genera of the Gentianaceae and that its systematic position was close to *Swertia* and *Lomatogonium*. It is at present impossible to assign *Obolaria* either to the Swertieae (Grisebach, 1839, 1845; Bentham & Hooker, 1876) or to the Gentianeae-Erythraeinae (Gilg, 1895). Neither our pollen morphological evidence nor gross morphology (Gillett, 1959) suggest a direct relationship between *Bartonia* and *Obolaria*. Our study may support Holm's idea (1897) of a relationship between *Obolaria* and *Swertia*, but it does not substantiate a close affinity between *Obolaria* and *Lomatogonium* with its different and characteristic type of pollen (Nilsson, 1964, 1967).

The taxonomic treatment of *Voyria*, *Leiphaimos*, and *Voyriella* has varied with time. Grisebach (1839) placed *Voyria* in the Lisiantheae and divided *Voyria* into two sections, *Leiphaimos* and *Lita*. In 1845 he added two more sections, *Leianthostemon* and *Pneumanthopsis*. Miquel (1849) described *Voyriella* as a new section of *Voyria* and in 1850 divided the Gentianeae parasiticae into a number of genera—*Voyria*, *Voyriella*, *Leiphaimos*, and others. Progel (1865) treated *Voyriella* and *Voyria* as genera, dividing the latter into a number of sections. Bentham and Hooker (1876) placed *Voyriella* and *Voyria sens. lat.* in the tribe Chironieae. Gilg (1895) placed *Voyria* in a tribe of its own, the Voyrieae, while *Voyriella* and *Leiphaimos* were placed in another tribe, the Leiphaimeae. Pollen grain characteristics were used to differentiate the two tribes. *Leiphaimos* was further subdivided into five sections. From anatomical studies, Svedelius (1902) agreed with Gilg that *Leiphaimos* and *Voyria* were not closely related. Raynal (1967), except for maintaining the type species *L. parasiticus*, found no evidence to maintain *Voyria* and *Leiphaimos* as distinct genera. Robyns (1968) treated *Voyria* in a broad sense with regard to the species occurring in Panama and, accordingly, made a transfer from *Leiphaimos* to *Voyria*.

We have found a close similarity between pollen of *Leiphaimos montanus* and *L. corymbosus*, which agrees with Jonker's (1936*b*) statement of a close relationship between the two species. The palynological similarity between *L. aphyllus* and *L. flavescens* seems to be without a gross morphological counterpart.

The pollen grains of *L. spruceanus* resemble those of *L. calycinus p.p.* and *Voyria rosea p.p.*, but the macromorphology of *L. spruceanus* differs from that of the other species (Jonker, personal communication). It is not yet possible to explain why *L. calycinus* and *Voyria rosea* show a comparable variation. Judging from a picture of *Voyria rosea* by Raynal (1967), the collections with radially symmetrical pollen grains could be regarded as *Voyria rosea*, the others as *Lei-*

phaimos calycinus. This cannot be fully confirmed until additional herbarium specimens have been studied. It should also be noted that one specimen of *L. calycinus* (*Versteeg 154*) is redetermined from *Voyria rosea* (Jonker, *in litt.*), which would be contrary to the above supposition.

L. tenellus and *L. aurantiacus* were placed together because of fusiform seeds (Miquel, 1850), and pollen morphology supports this. Jonker (1936*b*) placed *L. clavatus* in the genus *Voyria* instead of *Leiphaimos,* because of its comparatively large flowers. We have used the original name of *Voyria clavata* Splitg. in our study. Its pollen grains are similar to those of *V. caerulea* and *V. rosea,* but since we consider the pollen of *Voyria* and *Leiphaimos* to be essentially the same, with no distinct generic difference, we can only suggest a closer relationship between *V. clavata* and the above mentioned species examined of *Voyria sens. lat.*

Gilg (1895) included *Voyriella* together with *Leiphaimos* in his tribe Leiphaimeae and did not distinguish between the pollen grains of the two genera. Köhler (1905), following Gilg's taxonomic treatment, described the pollen grains of *Voyriella parviflora* as devoid of furrows and even pores (*cf.* Gilg, 1895) and with a smooth exine. Raynal (1967) noted that the pollen of *Voyriella* had short furrows with a central pore and thicker and more ornamented walls than *Voyria* and *Leiphaimos*. She gave several reasons for not placing *Voyriella* near *Voyria* and *Leiphaimos*.

We conclude from pollen morphology that *Voyriella* should better be associated with *Curtia* or *Enicostema* than with *Leiphaimos* (*cf.* Gilg, 1895). We also support the view of including *Leiphaimos* in *Voyria* (*cf.* Grisebach, 1839, 1845; Progel, 1864; Raynal, 1967; Robyns, 1968). The pollen grains of *Voyria* and *Leiphaimos* differ greatly from those of other Gentianaceae, and it is tempting to speculate whether or not the extreme simplicity of pollen in these taxa may be correlated with the saprophytic habit. The pollen grains of *Voyria* and *Leiphaimos* show too many resemblances to each other to be placed in different tribes as was done by Gilg (1895). Until a comprehensive revision is made it seems preferable to treat *Voyria* as an inclusive genus.

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CYTOTAXONOMIC NOTES ON SOME NEOTROPICAL GENTIANACEAE[1]

Richard E. Weaver, Jr.[2]

Abstract

Chromosome numbers for 13 species in four genera of neotropical Gentianaceae are reported for the first time. The chromosome numbers suggest a relationship between *Symbolanthus, Macrocarpaea,* and *Chelonanthus* and support the separation of *Lisianthius* and *Chelonanthus.*

The Gentianaceae is a moderate-sized family, comprising approximately 800 species (Engler & Diels, 1936). Their distribution is essentially worldwide. In many cases generic limits within the family are poorly defined, and intergeneric relationships are poorly understood. Particularly troublesome are those approximately 100 neotropical members of the family which are supposedly related to *Lisianthius* P. Browne. In accordance with the genera accepted by Gilg (1895) this would include the following: *Macrocarpaea* Gilg, *Pagaea* Griseb., *Helia* Mart., *Irlbachia* Mart., *Lehmaniella* Gilg, *Adenolisianthus* Gilg, *Calolisianthus* Gilg, *Chelonanthus* Gilg, *Purdieanthus* Gilg, *Lagenanthus* Gilg, *Rusbyanthus* Gilg, *Symbolanthus* Don, and *Lisianthius* P. Browne. Taxonomic studies of this group of genera have been hampered not only by the paucity of specimens, but also by their miserable condition. *Macrocarpaea* is the only genus of moderate size for which a reasonably complete monograph (Ewan, 1948) is available.

With the exception of *Gentiana* and its segregates, little is known about the cytology of the family. There are apparently no published chromosome counts for any of the lisianthioid genera. Counts are reported here for the first time for thirteen species in four of the genera. The standard squash technique was used: Flower buds were fixed in modified Carnoy's solution, stored in 70% ethanol, and the pollen mother cells were subsequently squashed in acetocarmine. The results are listed in Table 1.

According to the most comprehensive treatment of the Gentianaceae (Gilg, 1895), *Lisianthius* and *Macrocarpaea* belong to the tribe Gentianeae, subtribe Tachiinae, while *Chelonanthus* and *Symbolanthus* belong to the tribe Helieae. In Gilg's treatment the Gentianeae and the Helieae, as well as most other major groupings within the family, were delimited on the basis of pollen grain morphology. Those genera whose pollen grains are united into tetrads were referred to the Helieae; all other genera supposedly are characterized by having separate pollen grains.

The findings of more recent authors suggest that Gilg's system is probably inadequate. Ewan (1948) argued that the genera most closely related to *Macro-*

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TABLE 1. Chromosome numbers in four genera of neotropical gentians.

Species	Collection Data	Haploid number
Symbolanthus pulcherrimus Gilg	COSTA RICA. CARTAGO: 13 mi. SW of El Empalme, *Weaver 1406.*	$n = 40$ (Fig. 1)
Macrocarpaea thamnoides (Griseb.) Gilg	JAMAICA. ST. ANDREW: Fairy Glade on Mt. Horeb, *Weaver 952.*	$n = 21$ (Fig. 2)
Lisianthius capitatus Urb.	JAMAICA. TRELAWNY: Road from Burnt Hill to Barbecue Bottom, *Weaver 1002.*	$n = 18$
Lisianthius cordifolius L.	JAMAICA. ST. ANDREW: Gorge of the Cane River, *Weaver 878.*	$n = 18$ (Fig. 3)
Lisianthius exsertus Sw.	JAMAICA. ST. CATHERINE: 1 mi. S of Parks Road, *Weaver 1042.*	$n = 18$
Lisianthius jefensis Robyns & Elias	PANAMA. PANAMÁ: Cerro Jefe, *Weaver 1481.*	$n = 18$
Lisianthius latifolius Sw.	JAMAICA. ST. ANDREW: Morces Gap, *Weaver 1827.*	$n = 18$
Lisianthius longifolius L.	JAMAICA. TRELAWNY: Road from Burnt Hill to Barbecue Bottom, *Weaver 997.*	$n = 18$
Lisianthius seemannii (Griseb.) Perkins	PANAMA. COCLÉ: 3.5 km SE of El Valle de Antón, *Weaver 1671.*	$n = 18$
Lisianthius skinneri (Hemsl.) O. Kuntze	COSTA RICA. ALAJUELA: 13.5 mi. E of Arenal, *Wilbur & Stone 10257.*	$n = 18$
Lisianthius troyanus Urb.	JAMAICA. WESTMORELAND: 0.5 mi. S of Moreland Hill School, *Weaver 1272.*	$n = 18$
Lisianthius umbellatus Sw.	JAMAICA. HANOVER: Dolphin Head, *Weaver 1832.*	$n = 18$
Chelonanthus alatus (Aubl.) Pulle	PANAMA. COCLÉ: 3.5 km S of El Valle de Antón, *Weaver 1672.*	$n = 20$ (Fig. 4)
	PANAMA. PANAMÁ: Cerro Campana, *Weaver 1696.*	$n = 20$

carpaea, at least on the basis of gross morphology, are *Symbolanthus, Calolisianthus,* and *Rusbyanthus.* The last was placed by Gilg in a monotypic tribe between the Gentianeae and the Helieae; *Symbolanthus* and *Calolisianthus* were placed in the Helieae. Nilsson (1968) found three general types of pollen in the genus *Macrocarpaea,* two with separate grains and one with grains united into tetrads. Of the separate-grain types, one, found in three species, closely resembles the type found in *Rusbyanthus.* Those with pollen in tetrads, a group of five species restricted to Trinidad and Venezuela, are ones which, according to Ewan "often demonstrate transitional characters toward the morphology of the genera *Symbolanthus* and *Calolisianthus.*" According to Nilsson, however, the pollen most closely resembles that of *Chelonanthus.*

The cytological evidence at this point is too scanty to give more than a hint of the relationships between the genera in question. However, *Chelonanthus,* with $n = 20$ chromosomes (Fig. 4), may be the base for a polyploid series and an aneuploid series in the Helieae, leading to *Symbolanthus,* with $n = 40$ chromosomes (Fig. 1), in the former case, and to *Macrocarpaea,* with $n = 21$ (Fig. 2), in the latter. *Eustoma russellianum* G. Don, of the Gentianeae-Tachiinae, has

FIGURES 1 2.—Meiotic chromosomes of *Symbolanthus* and *Macrocarpaea*. — 1. *Symbolanthus pulcherrimus*, Metaphase I, × 1100. — 2. *Macrocarpaea thamnoides*, Metaphase I, × 1600.

$n = 36$ (Rork, 1949). *Lisianthius*, with $n = 18$ in all ten species investigated (Fig. 3), may be the base for a polyploid series in this subtribe.

Steyermark (1953) found no good morphological basis for maintaining *Chelonanthus* and suggested that it should be included in *Lisianthius*. Williams (1968), following Gilg (1895), pointed out several good corolla and inflores-

FIGURES 3–4.—Meiotic chromosomes of *Lisianthius* and *Chelonanthus*. — 3. *Lisianthius cordifolius*, Metaphase I, × 1500. — 4. *Chelonanthus alatus*, Metaphase I, × 1500.

cence characters for separating the two genera. Although a chromosome count is available for only one species of *Chelonanthus* ($n = 20$), the fact that all ten species of *Lisianthius* investigated have $n = 18$ chromosomes gives tentative support for the maintenance of *Lisianthius* and *Chelonanthus* as distinct genera.

The results of this study, meager though they may be, suggest that cytological data may prove valuable in determining generic limits and intergeneric relation-

ships in the lisianthioid gentians. However, much more work, cytological and otherwise, needs to be done before the taxonomy of these plants can be worked out with any confidence.

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SPORES OF THE HETEROPHYLLOUS *SELAGINELLAE* OF MEXICO AND CENTRAL AMERICA[1]

ROBERT LEE HELLWIG[2]

ABSTRACT

Megaspores and microspores of forty-six species and a presumed hybrid of heterophyllous *Selaginellae* from Mexico and Central America are described. Characters of the spores are correlated with three major groupings—the articulate group, the non-articulate group, and, within the latter, the group containing those species which curl into a ball when dried. A key based on spore and sporangial characters is included.

The genus *Selaginella* has attracted much attention from morphologists because of its heterospory, its stelar anatomy, and its controversial organ, the rhizophore. The genus is nearly worldwide in distribution, although most of the species are tropical. *Selaginella* is generally divided into two subgenera: homophyllous species are placed in subgenus *Selaginella;* heterophyllous species (having two dorsal rows of smaller leaves and two lateral rows of larger leaves) are placed in subgenus *Stachygynandrum*. The latter has been further divided on the basis of habit, articulation of the stems, arrangement of the leaves, and geographical distribution (Greville & Hooker, 1831; Spring, 1850; Braun, 1860; Baker, 1883; Hieronymus, 1902; Alston, 1955). Stem articulation in *Selaginella* is presumed rather than real. At each node (site of stem ramification) in the "articulate" species there is a narrow constriction or discoloration of the main stem that is suggestive of an abscission layer.

Alston (1955) prepared a key to the heterophyllous species of *Selaginella* of North America south to Panama. He grouped the species largely according to the characters used in previous classifications but occasionally made use of spore characteristics to separate difficult groups. The spore characters he used are color of both megaspores and microspores and ornamentation of the microspores. Tryon (1949) described the spores of the American species of *Selaginella* which occur north of Mexico. These are largely homophyllous species.

Unpublished work by Mickel shows that the heterophyllous *Selaginellae,* which are mostly tropical, are more diverse in spore morphology than the homophyllous species. The present study describes the spores of the heterophyllous species of Mexico and Central America, especially with regard to color, size, and ornamentation. This information will be correlated with previous taxonomic groupings. This study is preliminary in nature and will undoubtedly be corrected and amplified by further investigation of this group.

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[1] Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science, Iowa State University, Ames, Iowa. I thank Dr. John T. Mickel for pointing out the problem and for his assistance in the course of the study.

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TABLE 1. Specimens on which the descriptions of spores are based.

Selaginella anceps.
COSTA RICA: *Mickel 2696* (NY).
Selaginella arthritica.
COSTA RICA: *Mickel 3334* (NY).
Selaginella articulata.
PANAMA: *Lewis, MacBryde, Oliver & Ridgway 1777* (MO).
Selaginella bombycina.
PANAMA: *Allen 2225* (MO).
Selaginella cladorrhizans.
MEXICO: *Mexia 8725* (MO, NY).
Selaginella delicatissima.
MEXICO: *Mickel 1114* (ISC).
Selaginella estrellensis.
COSTA RICA: *Stork 1755* (MO).
GUATEMALA: *Cooper 6062* (NY).
Selaginella eurynota.
COSTA RICA: *Brenes 5783* (NY); *Skutch 2216* (MO).
Selaginella exaltata.
COSTA RICA: *Mickel 1988* (NY).
Selaginella flagellata.
COLOMBIA: *Smith 2245* (ISC).
Selaginella galeottii.
MEXICO: *Mickel 894* (ISC).
Selaginella guatemalensis.
HONDURAS: *Yuncker, Dawson & Youse 5840* (MO).
GUATEMALA: *Maxon & Hay 3297* (NY).
Selaginella haematodes.
PANAMA: *Burch, Oliver & Solis 1079* (MO).
Selaginella hoffmannii.
MEXICO: *Hellwig 467* (ISC).
Selaginella horizontalis.
PANAMA: *Allen 2013* (NY); *Johnston 1142* (MO).
Selaginella huehuetenangensis.
PANAMA: *Smith & Smith 3305* (ISC).
GUATEMALA: *Standley 24173* (NY).
Selaginella idiospora.
COSTA RICA: *Mickel 3276* (NY).
Selaginella illecebrosa.
GUATEMALA: *Steyermark 41579* (US).
Selaginella intacta.
COSTA RICA: *Mickel 2645* (NY).
Selaginella kunzeana.
COSTA RICA: *Jimenez 1706* (NY); *Skutch 3106* (MO).
Selaginella lepidophylla.
MEXICO: *Knobloch 1919* (ISC); *Pringle 5417* (ISC).
Selaginella lychnuchus.
MEXICO: *Palmer 265* (MO).
COSTA RICA: *Mickel 2310* (ISC).
Selaginella marginata.
MEXICO: *Pennell 20187* (US).
Selaginella martensii.
MEXICO: *Mickel 948* (ISC).
Selaginella microdendron.
MEXICO: *Rzedowski 10670* (ISC).
BRITISH HONDURAS: *Schipp 99* (NY).
Selaginella minima.
PANAMA: *Johnston 878* (US).
Selaginella mollis.
COSTA RICA: *Molina, Williams, Burger & Wallenta 17144* (NY).
Selaginella novae-hollandiae.
PANAMA: *Burch, Oliver & Solis 1088* (MO, NY).
Selaginella novoleonensis.
MEXICO: *King 4559* (ISC, NY).
Selaginella oaxacana.
MEXICO: *Mickel 947* (ISC).
Selaginella ovifolia.
BRITISH HONDURAS: *Schipp 924* (US).
Selaginella pallescens.
MEXICO: *Mickel 1169* (ISC).
Selaginella porphyrospora.
MEXICO: *Mickel 1560* (NY).
Selaginella pulcherrima.
MEXICO: *Conzatti 807* (US).
Selaginella reflexa.
MEXICO: *Pringle 10326* (NY).
Selaginella revoluta.
COLOMBIA: *Hermann 10975* (US).
VENEZUELA: *Williams 11379* (US).
Selaginella schaffneri.
MEXICO: *Pringle 15630* (US); *Schaffner 8* (NY).
Selaginella schiedeana.
MEXICO: *Pringle 5415* (ISC).
Selaginella schizobasis.
MEXICO: *Ghiesbreght 605* (NY).
Selaginella sertata.
MEXICO: *Rzedowski 14912* (NY).
Selaginella silvestris.
HONDURAS: *Yuncker, Koepper & Wagner 8490* (MO).
COSTA RICA: *Kuntze 2014* (NY).
Selaginella stenophylla.
MEXICO: *Mickel 625* (ISC).
Selaginella tarapotensis.
MEXICO: *Mickel 956* (ISC); *Mickel 946* (NY).
Selaginella umbrosa.
BRITISH HONDURAS: *Wilson 217* (NY).
Selaginella unknown species 1.
MEXICO: *Mickel 1086* (NY).
Selaginella unknown species 2.
MEXICO: *Mickel 1579* (NY).
Presumed hybrid.
MEXICO: *Rzedowski & McVaugh 5* (NY).

Materials and Methods

This study is based on materials obtained from the herbaria of Iowa State University, the New York Botanical Garden, the United States National Museum, and the Missouri Botanical Garden. The specimens on which the descriptions are based are listed in Table 1. The author expresses appreciation to the curators of these herbaria for making specimens available.

Basically the species in this study are those found in Alston's key (1955). Excluded are a few species which are limited to North America north of Mexico. Material of some species treated by Alston was not available. Also missing are species specimens of which lacked cones, had shed their spores, or had immature spores. Despite these deficiencies 46 species and a presumed hybrid from Mexico were examined.

In this preliminary study, spores from one specimen, if both megaspores and microspores were present, were used to avoid possible confusion should the specimen later be found to be misidentified. Spores were removed from the strobili (from naturally opened sporangia in most cases) and placed on white paper. They were observed at 10 × and color was determined according to Ridgway (1912). In the descriptions the color from Ridgway is followed by a vernacular equivalent, if the color is not obvious from the formal name. The spores were then directly mounted and cleared in Hoyer's medium (Anderson, 1954) and dried on a heating tray at 56° C.

Spore measurements were made from the preparations using a Leitz Labolux microscope fitted with an ocular micrometer. Different magnifications were used for the various sizes of spores. An attempt was made to measure 20 free microspores from each species. The number of megaspores measured depended on the number readily available. In the spore descriptions the three measurmenets are the minimum, the average (*italicized*), and the maximum spore sizes respectively. The diameter of the megaspores, excluding the muri, was measured; the spines and other projections were not included in the measurements of the microspores. The drawings were done with the aid of a Zeiss drawing apparatus.

Spore Descriptions

The spores of the heterophyllous *Selaginellae* are tetrahedral with a triradiate scar on the proximal face. The megaspores are generally marked by undulating, anastomosing muri or ridges which may form flanges at the equator and/or along the scar. High muri range from 100–150μ; low muri are from 15–50μ in height. There is generally less ornamentation on the proximal face than on the distal face. The microspores generally have papillae or spines, rarely ridges. Terms for the wall layers, such as exospore and perispore, have been purposely avoided, since the origin of the wall layers is a matter of controversy. The outer part of the high muri is of a granular, more translucent material than that of the base. In many species the megaspore wall has very fine markings that are seen both in the areoles and beneath the muri suggesting that the muri are of a different nature.

The sporangia of *Selanginella* are generally arranged in four vertical rows in the strobili. Horner and Arnott (1963) have shown the taxonomic significance of the patterns of sporangial distribution. Therefore, the patterns of distribution are noted. The patterns include: one basal megasporangium per strobilus; two longitudinal rows of megasporangia and two longitudinal rows of microsporangia per strobilus; wholly megasporangiate or microsporangiate strobili; and various mixed patterns.

In order to facilitate comparison of taxonomic groupings and previous descriptive works, the sequence of presentation is that of Alston's key (1955). The spores are described with reference to color, size, and ornamentation as in Tryon (1949), and notes on sporangial distribution and other pertinent features are

added when possible. A provisional key to the species considered in this study is provided.

Non-Articulate Species

Selaginella novoleonensis Hieron.

Megaspores. Cadmium Yellow (gold); 127–326–382μ in diameter, 10 spores measured; muri quite high on both faces with extensions forming flanges and high curved peaks at some places; spores from each sporangium highly variable in size; strobili with two longitudinal rows of each type of sporangium (Fig. 13–14).

Microspores. Bittersweet Orange (highly variable); tetrad size 69–79–91μ in diameter, 10 tetrads measured, individual spore outline as seen through outer wall about 25μ in diameter; common wall around the spores undulate and fluted at one end, nearly smooth at the other (Fig. 52).

Selaginella lepidophylla (Hook. & Grev.) Spring.

Megaspores. Lemon Chrome (yellow); 245–321–413μ in diameter, 5 spores measured; with high irregular ridges on both proximal and distal faces, often elongate into spines. Strobili mixed; most of the sporangia microsporangiate.

Microspores. Mikado Orange; tetrad 76–79–87μ in diameter, 4 tetrads measured, individual spore outlines 32–39μ in diameter. Spores shed in tetrads surrounded by a common, heavily undulate wall.

Selaginella pallescens (Presl) Spring.

Megaspores. Clay Color; 387–418–448μ in diameter, 4 spores measured; ridges thin and vein-like; megasporangia in the lower part of the strobili (Fig. 7–8).

Microspores. Scarlet; 21–22–24μ in diameter, 20 spores measured; papillae short, capitate.

Selaginella microdendron Baker.

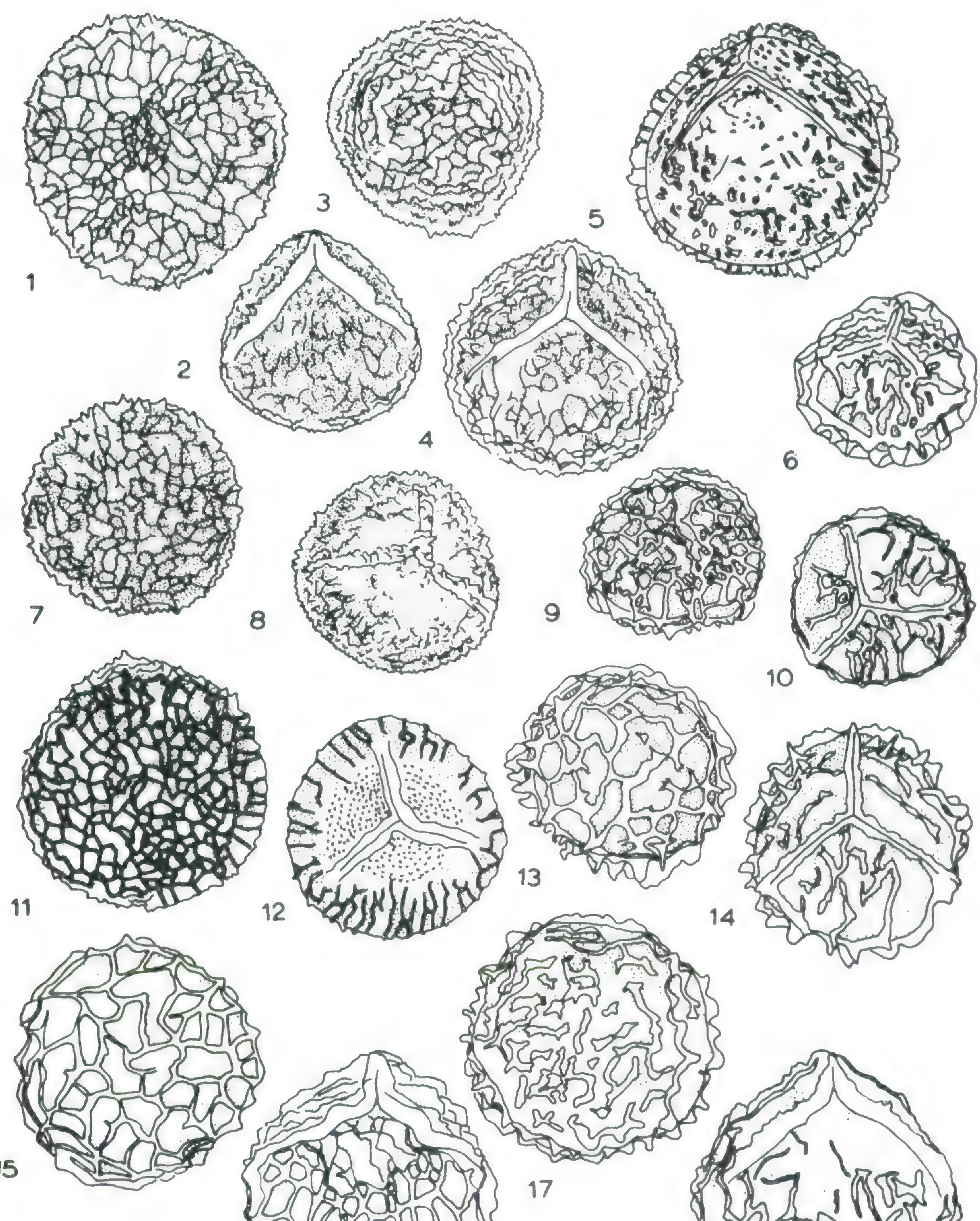
Megaspores. Pale Ochraceous Buff (very pale orange); 306–352–392μ in diameter, 6 spores measured; with low, broad ridges, even on proximal face; strobili loosely constructed of a few sporophylls, no constant pattern of sporangial arrangement.

Microspores. Orange; heavy capitate papillae.

Selaginella umbrosa Lemaire *ex* Hieron.

Megaspores. White; 209–224–240μ in diameter, 10 spores measured; with low ridges; spores extremely thin-walled with all the larger ones breaking, the measurements are therefore too low; megasporangia and microsporangia in two longitudinal rows.

Microspores. Bittersweet Orange; 20–22–24μ in diameter, 20 spores measured; with sparse, short papillae (Fig. 32–33).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Selaginella haematodes (Kunze) Spring.

Megaspores. Maize Yellow (off-white); 204–235–296μ in diameter, 6 spores measured; ridges low to medium in height; strobili with two rows of megasporangia and two rows of microsporangia.

Microspores. Light Salmon-Orange; 21–23–29μ in diameter, 20 spores measured; with sparse, rounded to capitate papillae.

Selaginella hoffmannii Hieron.

Megaspores. White; 240–275–316μ in diameter, 7 spores measured; with low ridges; strobili possibly with two rows of microsporangia together and two rows of megasporangia opposite them.

Microspores. Grenadine Red (bright orange); 21–28–31μ in diameter, 20 spores measured; ridges narrow with occasional blunt spine-like projections.

Selaginella bombycina Spring.

Megaspores. White; 306–316–326μ in diameter, 5 spores measured; with low ridges; strobili with two rows of each type of sporangium, some exceptions noted.

Microspores. Bittersweet Orange; 29–36–40μ in diameter, 20 spores measured; with low capitate papillae.

Selaginella anceps Presl.

Megaspores. White; 235–245–260μ in diameter, 7 spores measured; with low narrow ridges; spores break very easily; very few megasporangia per strobilus.

Microspores. Salmon-Orange; 22–24–26μ in diameter, 20 spores measured; papillae small; many spores of irregular shape.

Selaginella oaxacana Spring.

Megaspores. Cream Color; 362–382–413μ in diameter, 4 spores measured; distal face with low narrow ridges, proximal face with granular emergences to papillae (Fig. 11–12).—There is some tendency toward inequality of spore size in any one sporangium. The megasporangia make up the basal half of the strobilus.

Microspores. Bittersweet Orange; 21–23–26μ in diameter, 14 spores measured; with few broad, short papillae; most of the spores in tetrads.

Selaginella pulcherrima Liebm. & Fourn.

Megaspores. Pale Orange-Yellow (beige); 300–338–398μ in diameter, 3 spores measured; with low, narrow ridges, minute papillae between and on ridges,

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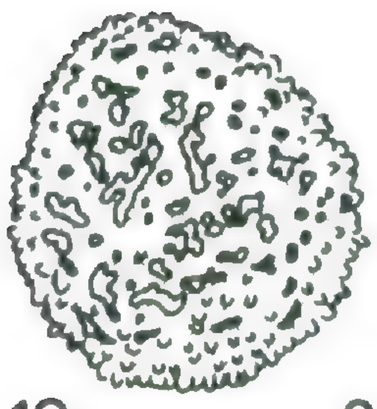
FIGURES 1–18.—Megaspores of *Selaginella.* — 1–2. *S. guatemalensis,* × 120.—1. Distal face.—2. Proximal face. — 3–4. *S. idiospora,* × 120.—3. Distal face.—4. Proximal face. — 5. *S. schaffneri,* proximal face, × 120. — 6. *S. porphyrospora,* proximal face, × 120. — 7–8. *S. pallescens,* × 120.—7. Distal face.—8. Proximal face. — 9–10. *S. stenophylla,* × 120. 9. Distal face.—10. Proximal face. — 11–12. *S. oaxacana,* × 120.—11. Distal face.—12. Proximal face. — 13–14. *S. novoleonensis,* × 120. —13. Distal face. —14. Proximal face. — 15–16. *S. mollis,* × 125.—15. Distal face.—16. Proximal face. — 17–18. *S. tarapotensis,* × 125.—17. Distal face.—18. Proximal face.



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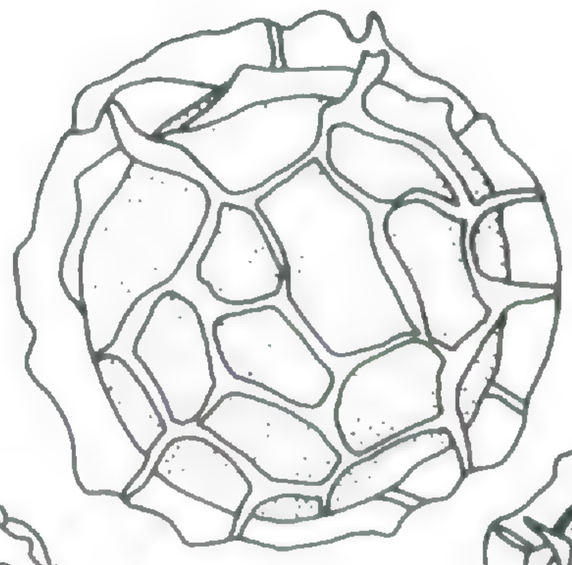

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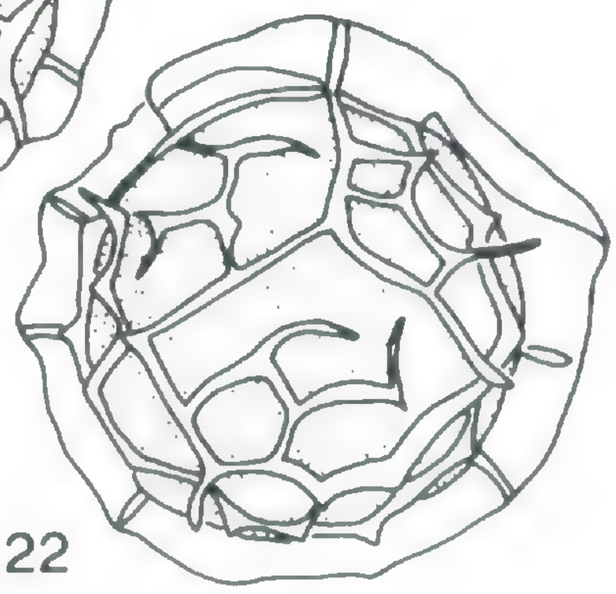

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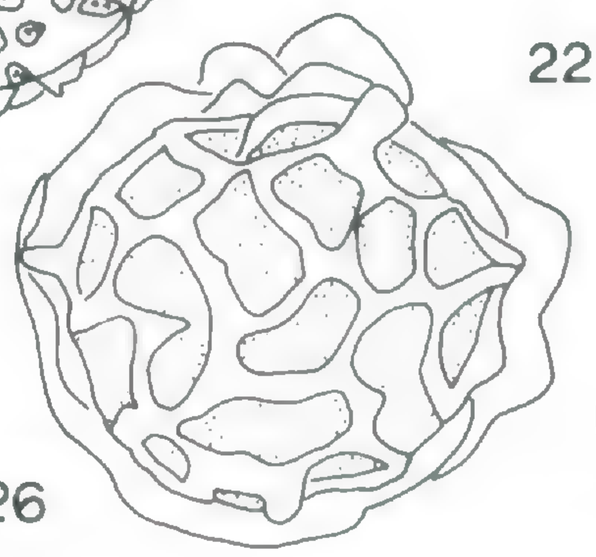

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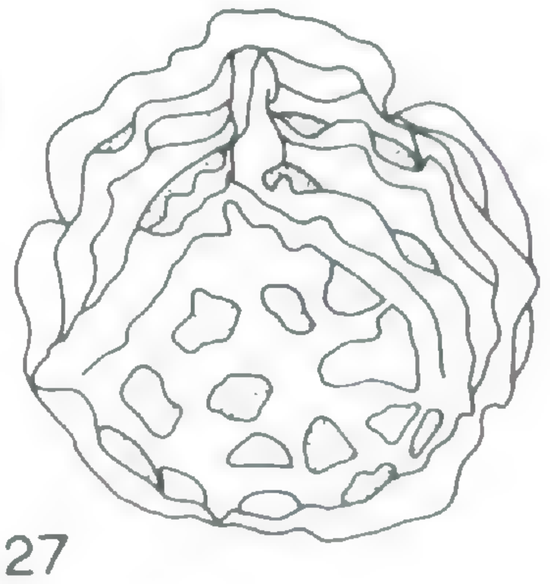

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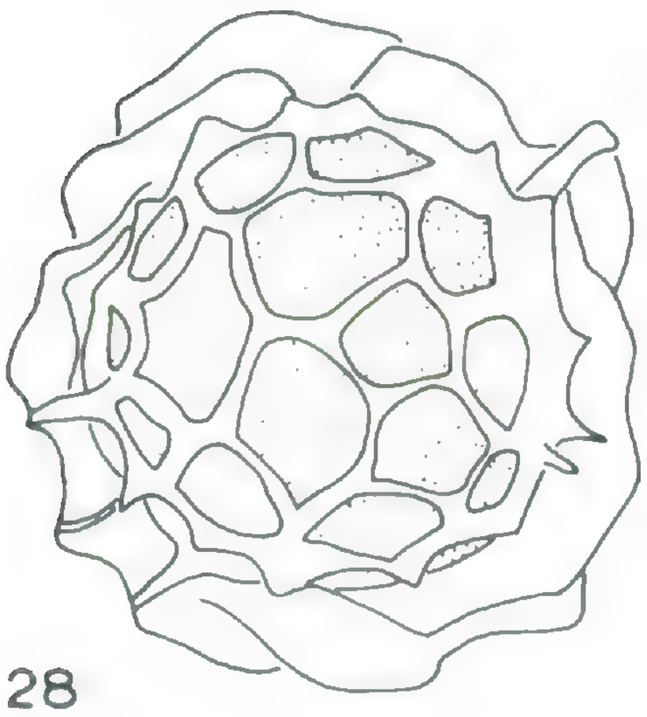

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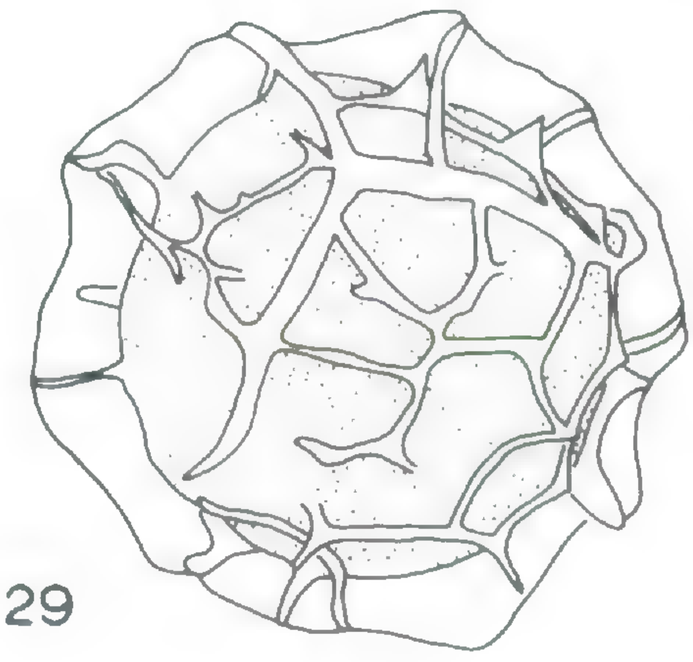

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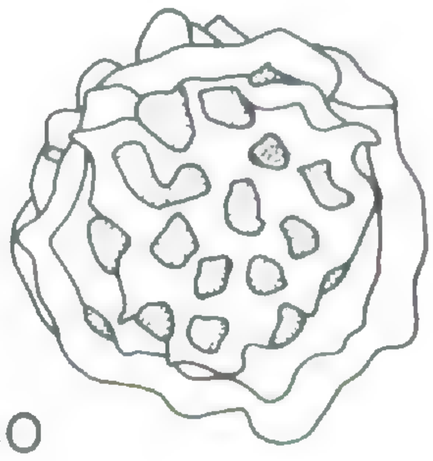

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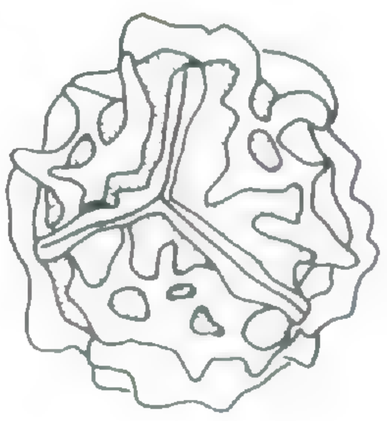

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and on proximal face; few microsporangia in each strobilus.

Microspores. Bittersweet Orange; 26–30–36μ in diameter, 20 spores measured; sparingly papillose.

Selaginella illecebrosa Alston.

Megaspores. Pale Yellow-Orange (beige); 245–292–321μ in diameter, 10 spores measured; ridges of medium height.—The bottom half of the strobilus appears to be megasporangiate with very few microsporangia in the upper half.

Microspores. Xanthine Orange (orange-brown); 19–20–23μ in diameter, 20 spores measured; with large rounded or capitate papillae; some spores remaining in tetrads.

Selaginella schaffneri Hieron.

Megaspores. Grenadine Pink (orange) with white ridges; 367–402μ in diameter, 2 spores measured; ridges low to medium in height, uneven, sparsely anastomosing (Fig. 5).—Many spores broke in preparation. There are a few basal megasporangia per strobilus, and the rest of the strobilus contains a few microsporangia very close to the lower part or distant from it.

Microspores. Bittersweet Pink, Light Salmon Orange, Bittersweet Orange, and Salmon Orange; 47–56–63μ in diameter, 20 spores measured; heavy, broad ridges cover most of the distal face, leaving a few cavities; spores often in tetrads (Fig. 55–56).

Selaginella delicatissima Linden.

Megaspores. Empire Yellow (dark yellow); 443–473–494μ in diameter, 3 spores measured; with low papillae merging to form short, irregular ridges; unequally-sized spores in each sporangium; megasporangia generally located in the lower half of the strobilus (Fig. 19–20).

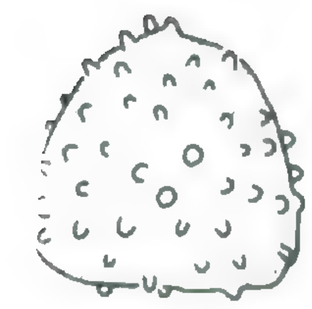
Microspores. Orange Chrome; 40–47–55μ in diameter, 20 spores measured; ornamentation highly variable, ranging from densely papillose to irregularly ridged, on both faces (Fig. 57–59).

Selaginella tarapotensis Baker.

Megaspores. Cream Color; 255–275–291μ in diameter, 6 spores measured; with very low ridges; many broken open in preparation; megasporangia basal (Fig. 17–18).

Microspores. Bittersweet Orange; 25–28–29μ in diameter, 20 spores measured; papillae slender to capitate (Fig. 36–37).

FIGURES 19–31.—Megaspores of *Selaginella.* — 19–20. *S. delicatissima,* × 60.—19. Distal face.—20. Proximal face. — 21–22. *S. sertata,* × 60.—21. Distal face.—22. Proximal face. — 23–24. *S. intacta,* × 60.—23. Distal face.—24. Proximal face. — 25. Presumed hybrid, × 60. — 26–27. *S. arthritica,* × 60.—26. Distal face.—27. Proximal face. — 28–29. *S. exaltata,* × 30.—28. Distal face.—29. Proximal face. — 30–31. *S. articulata,* × 30. —30. Distal face.—31. Proximal face.



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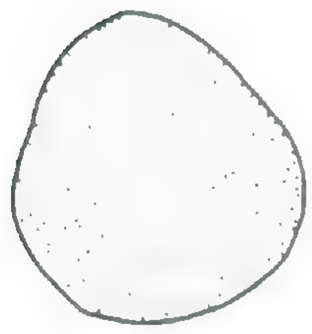

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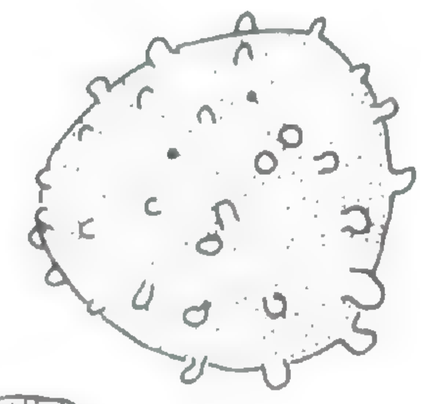

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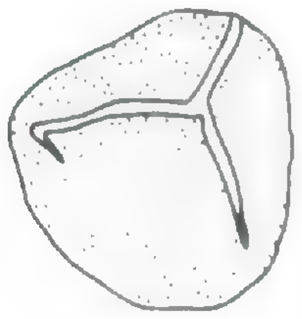

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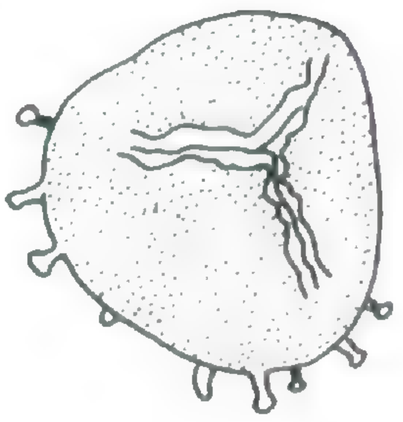

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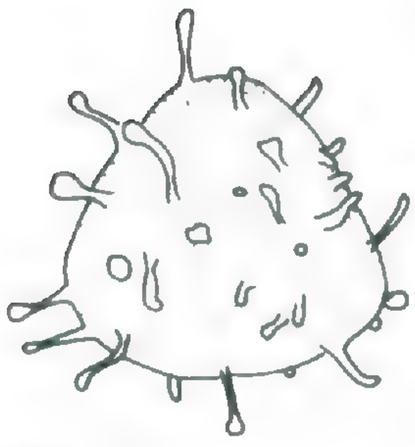

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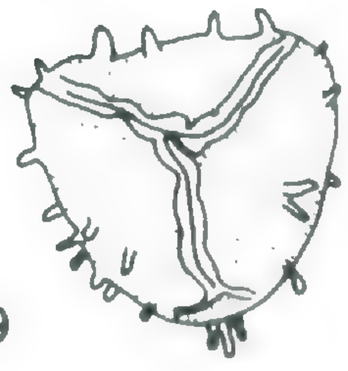

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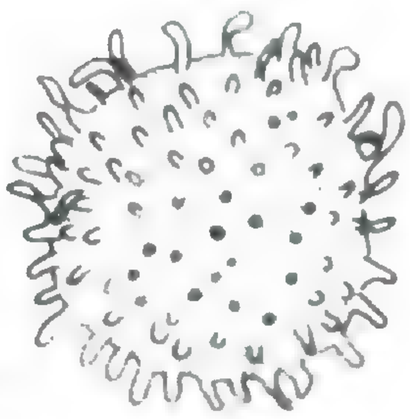

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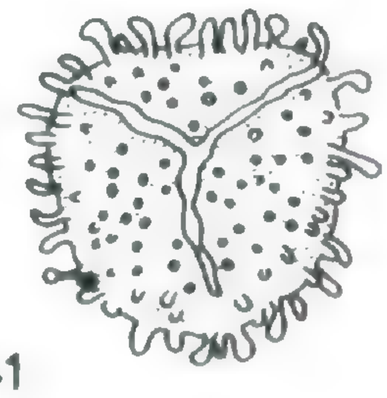

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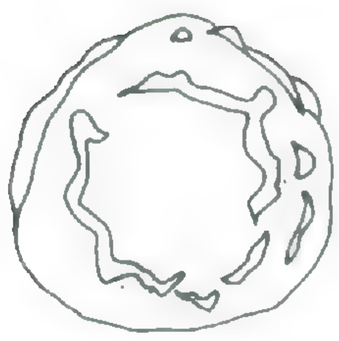

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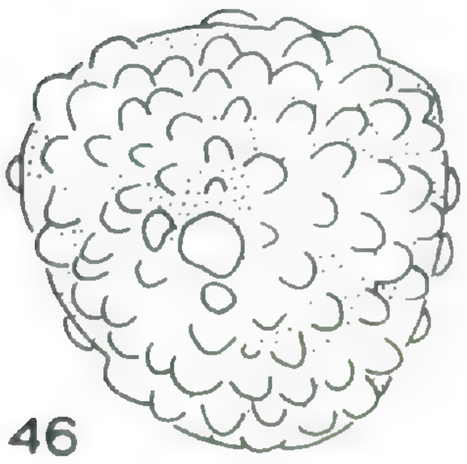

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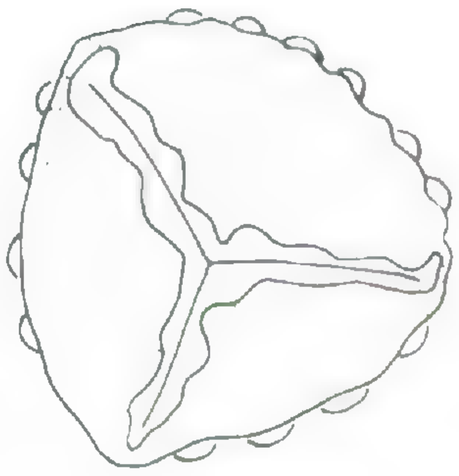

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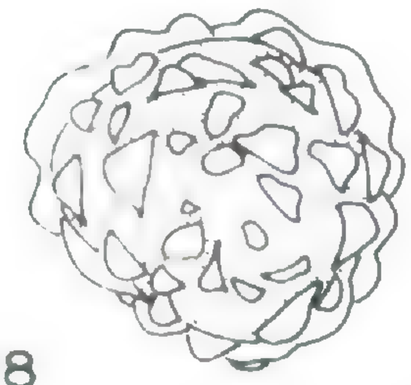

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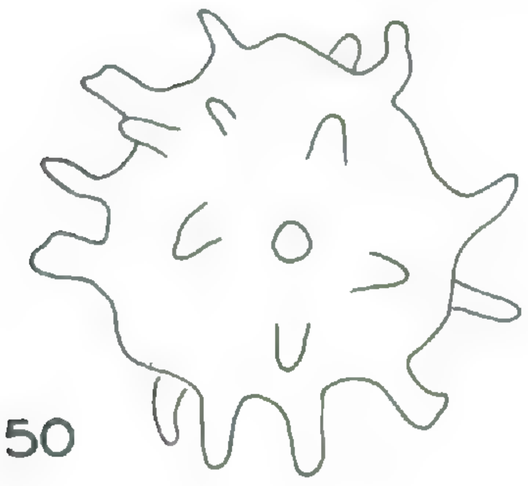

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51

Selaginella ovifolia Baker.

Megaspores. Cream Buff (beige); 219–224–240μ in diameter, 4 spores measured; ridges low.

Microspores. Flame Scarlet; 30–36–39μ in diameter, 20 spores measured; with short, broad papillae (Fig. 46–47).

Selaginella reflexa Underw.

Megaspores. Picric Yellow; 321–336–367μ in diameter, 5 spores measured; with broad muri of medium height extending to triradiate crest; tendency toward unequally-sized spores; very few microsporangia.

Microspores. Bittersweet Orange; 29–32–36μ in diameter, 20 spores measured; ridge-like papillae highly irregular in size and shape, apparently at least partially abortive (Fig. 48–49).

Selaginella guatemalensis Baker.

Megaspores. Light Buff (pale orange); 342–377–458μ in diameter, 4 spores measured; with low ridges; most spores broken in preparation; megasporangia basal (Fig. 1–2).

Microspores. Pale Orange-Yellow (beige); 24–28–31μ in diameter, 20 spores measured; high narrow ridges (Fig. 44–45).

Selaginella huehuetenangensis Hieron.

Megaspores. White; 316–372–407μ in diameter, 8 spores measured; wall marked by a reticulate pattern, but ridges lacking; megasporangia basal.

Microspores. Bittersweet Orange; 23–26–31μ in diameter, 20 spores measured; with narrow ridges and elongate spine-like projections.

Selaginella idiospora Alston.

Megaspores. Light Cinnamon Drab (brown-gray); 321–362–392μ in diameter, 10 spores measured; ridges low with very fine networks or papillae within the areoles; megasporangia few and basal (Fig. 3–4).

Microspores. Salmon-Buff (pale orange); 23–24–26μ in diameter, 20 spores measured; with low, broad papillae with hints of narrow, interconnecting ridges (Fig. 42–43).—Many spores are in tetrads, as Alston (1955) mentions in his key.

Selaginella revoluta Baker.

Megaspores. Cream Color; 275–281μ in diameter, 2 spores measured; with narrow, uncrowded muri of medium height; most spores broken in preparation.—

FIGURES 32–51.—Microspores of *Selaginella.* — 32–33. *S. umbrosa,* × 600.—32. Distal face.—33. Proximal face. — 34–35. *S. revoluta,* × 600.—34. Distal face.—35. Proximal face. — 36–37. *S. tarapotensis,* × 600.—36. Distal face.—37. Proximal face. — 38–39. *S. flagellata,* × 600.—38. Distal face.—39. Proximal face. — 40–41. *S. exaltata,* × 600.—40. Distal face.—41. Proximal face. — 42–43. *S. idiospora,* × 600.—42. Distal face.—43. Proximal face. — 44–45. *S. guatemalensis,* × 600.—44. Distal face.—45. Proximal face. — 46–47. *S. ovifolia,* × 600.—46. Distal face.—47. Proximal face. — 48–49. *S. reflexa,* × 600.—48. Distal face.—49. Proximal face. — 50–51. *S. marginata,* × 600.—50. Distal face.—51. Proximal face.

The strobili are almost totally megasporangiate with only one microsporangium at the top.

Microspores. Flame Scarlet; 22–25–28μ in diameter, 20 spores measured; no markings (Fig. 34–35).—Perhaps the spores were immature, although they were all separate.

Selaginella schiedeana A. Braun.

Megaspores. Pinard Yellow; 331–402–469μ in diameter, 10 spores measured; with narrow ridges of medium height; three small spores and one large one in each sporangium.—There are a few basal megasporangia per strobilus.

Microspores. Grenadine Red (bright orange); 29–42–56μ in diameter, 20 spores measured; with short, broad papillae, even on the proximal face; many irregular in size and shape (Fig. 53–54).

Selaginella cladorrhizans A. Braun.

Megaspores. Yellow; 202–210–218μ in diameter, 4 spores measured; ridges often peaked; strobili with two longitudinal rows of each type of sporangium.

Microspores. Flame Scarlet, 25–28–31μ in diameter, 20 spores measured; with stoutly capitate projections.

Selaginella lychnuchus Spring *ex* Klotzsch.

Megaspores. Light Buff (pale orange); 296–311–336μ in diameter, 9 spores measured; with ridges low, sparsely anastomosing, with frequent papillae on the ridges; two rows of each type of sporangium.

Microspores. Grenadine (orange); 24–28–31μ in diameter, 20 spores measured; papillae low and broad to capitate; many spores in tetrads.

Selaginella stenophylla A. Braun.

Megaspores. Avellaneous (brown); 255–286–316μ in diameter, 10 spores measured; with low, narrow ridges (Fig. 9–10).—The strobili seem to be made up of a few megasporangia at the base and microsporangia above.

Microspores. Bittersweet Orange; 24–28–32μ in diameter, 20 spores measured; with sparse low, narrow ridges; all spores in tetrads.

Selaginella martensii Spring.

Megaspores. White; 347–387–418μ in diameter, 10 spores measured; with low ridges.—The lower half of the strobilus appears to be megasporangiate and the upper half microsporangiate.

Microspores. Flame Scarlet; 21–23–26μ in diameter, 11 spores measured; with few, low, broad papillae which occasionally coalesce into ridges; many in tetrads.—The spores were perhaps immature.

Selaginella estrellensis Hieron.

Megaspores. Pale Ochraceous Buff (very pale orange); 306–377–484μ in diameter, 6 spores measured; with very low, narrow ridges, minute papillae on and between the ridges; megasporangia basal.—The larger spores were broken in preparation, so the measurements more strongly reflect the smaller two spores of each sporangium.

Microspores. Pale Orange-Yellow; 23–25–29μ in diameter, 20 spores measured.—Most of the spores were in tetrads with only slight markings and were probably immature.

Selaginella mollis A. Braun.

Megaspores. Cream Color; 255–270–301μ in diameter, 7 spores measured; with low, narrow ridges (Fig. 15–16).—The strobili are made up largely of megasporangia with a few microsporangia at the top.

Microspores. Bittersweet Orange; 21–23–28μ in diameter, 20 spores measured; papillae short.

Selaginella minima Spring.

Megaspores. White; 260–270–275μ in diameter, 8 spores measured; with low, narrow ridges.

Microspores. None found.

Selaginella porphyrospora A. Braun.

Megaspores. Bittersweet Orange; 205–255μ in diameter, 2 spores measured; with broad muri of medium height (Fig. 6).—Most of the spores were broken in preparation. The megasporangia predominate with the microsporangia in no particular part of the strobilus.

Microspores. Capucine Orange; 43–47–55μ in diameter, 20 spores measured; walls very thin, decorated with a granular material; mostly broken.

Selaginella novae-hollandiae (Sw.) Spring.

Megaspores. Off-white; 188–202–218μ in diameter, 8 spores measured; strobili with very few, basal megasoprangia.

Microspores. Bittersweet Orange; 18–19–21μ in diameter, 10 spores measured; with long, slender, capitate projections; mostly shed in tetrads.

Selaginella flagellata Spring.

Megaspores. Cream Color; 214–224–240μ in diameter, 6 spores measured; with low, narrow ridges.—The lower half of the strobilus is megasporangiate.

Microspores. Mikado Orange; 22–25–26μ in diameter, 20 spores measured; with long, slender, capitate papillae (Fig. 38–39).

Selaginella unknown species 1.

Megaspores. White; 194–235–255μ in diameter, 10 spores measured; with low, narrow ridges.

Microspores. Capucine Yellow (orange); 22–24–26μ in diameter, 20 spores measured; papillae short and broad or elongate and slightly capitate.

Selaginella unknown species 2.

Megaspores. Cream Color; 255–291–342μ in diameter, 10 spores measured; with low, narrow ridges.

Microspores. Chrome Orange; 25–29–31μ in diameter, 20 spores measured; with long, thin, capitate papillae.

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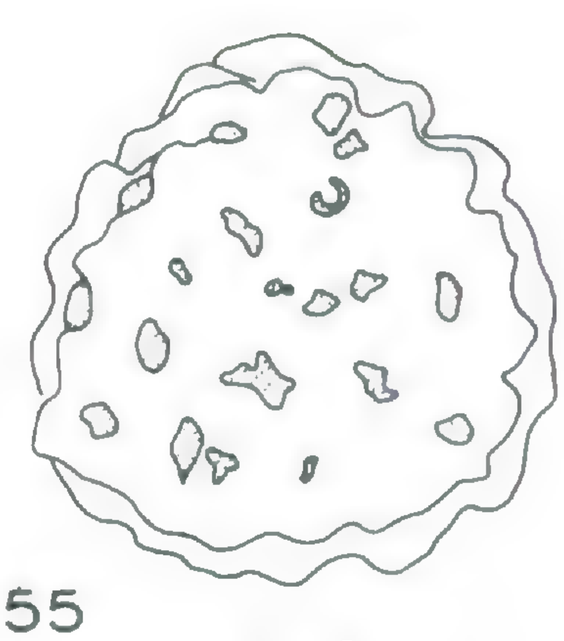
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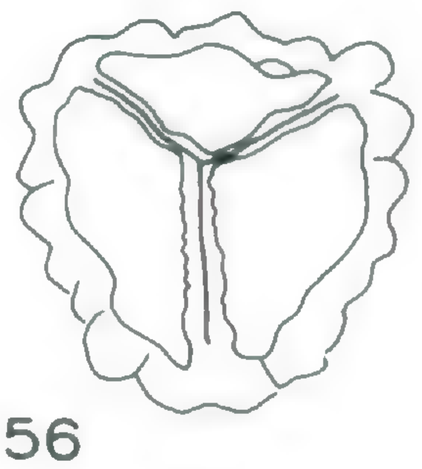
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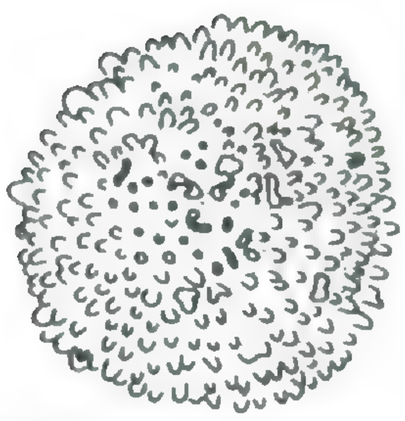
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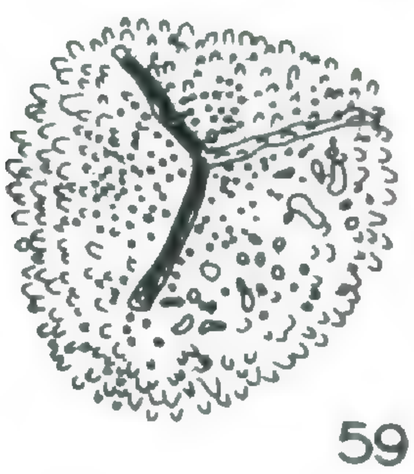
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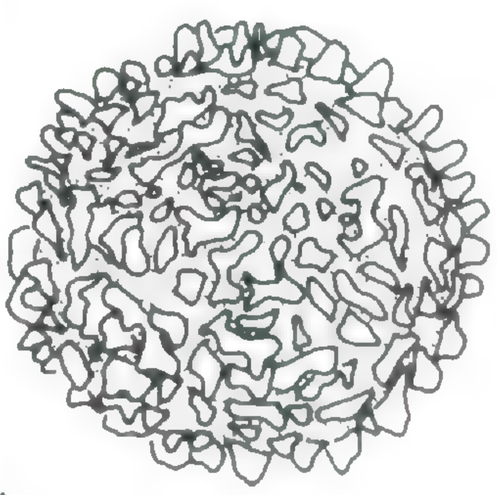
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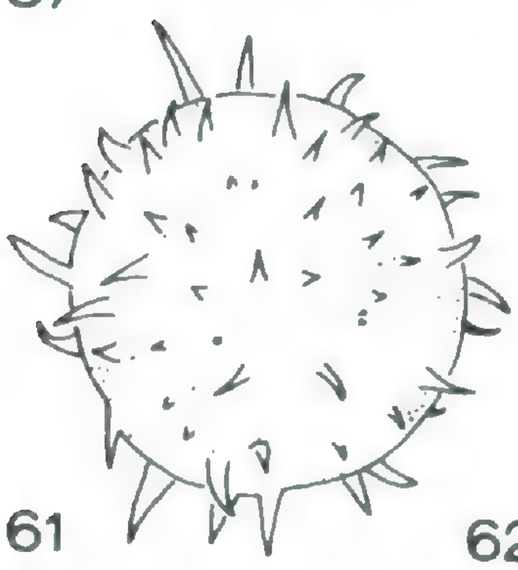
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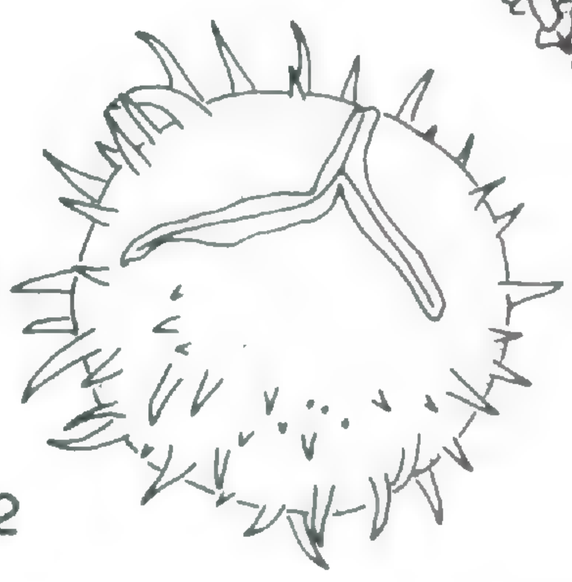
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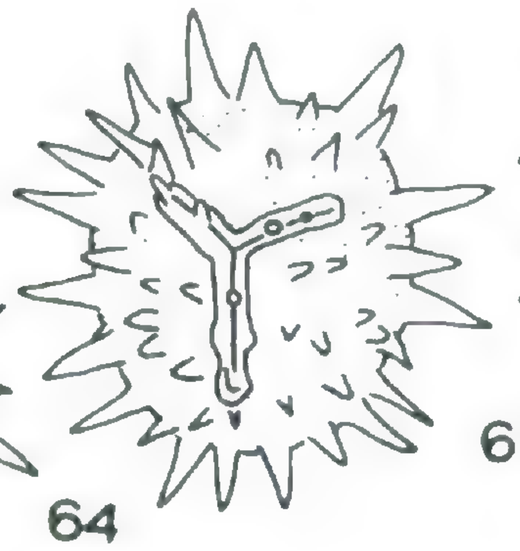
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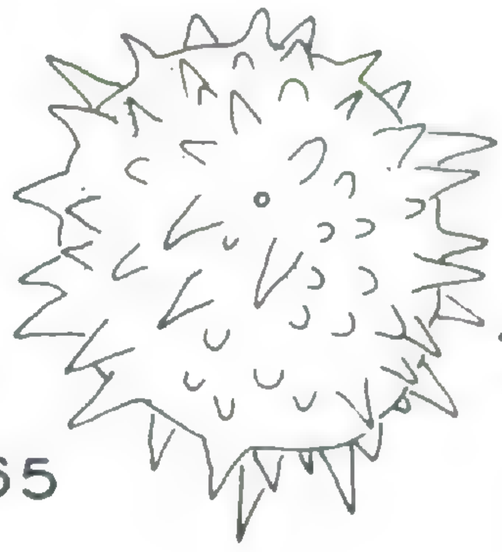
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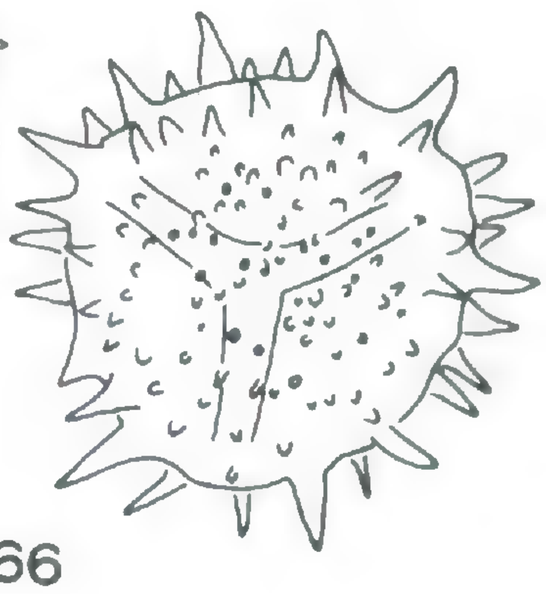
66

Presumed hybrid.

Megaspores. Cream Color; 646–*803*–1019μ in diameter, 4 spores measured; variously marked with irregular ridges; spores very irregular in shape and size; one spore per sporangium; one or two megasporangia at the base of each strobilus (Fig. 25).

Microspores. Flame Scarlet; spores mostly abortive; walls marked with heavy, irregular bumps and ridges (Fig. 60).—This collection is presumably a hybrid between *Selaginella pallescens* and some unknown species. The spores are mostly abortive and the plants similar to *S. pallescens,* though they do not fit the characters of that species or any other known to me. Hybridization has been little studied in *Selaginella,* so this collection is specially noteworthy.

Articulate Species

Selaginella exaltata (Kunze) Spring.

Megaspores. Salmon-Orange (pale orange) with off-white ridges; 1,058–*1,117*–1,176μ in diameter, 10 spores measured; with high, narrow muri and irregular thickenings in areoles and on the muri (Fig. 28–29).—There is one basal megasporangium per strobilus.

Microspores. Light Buff (sand); 22–25–28μ in diameter, 20 spores measured; with many, slender, somewhat capitate projections (Fig. 40–41).

Selaginella articulata (Kunze) Spring.

Megaspores. Ochraceous-Salmon (beige) with white ridges; 529–568–588μ in diameter, 4 spores measured; high, broad ridges (Fig. 30–31).—There is one basal megasporangium per strobilus.

Microspores. Light Buff (sand); 22–25–29μ in diameter, 20 spores measured; with spines (Fig. 63–64).

Selaginella arthritica Alston.

Megaspores. Light Buff (sand) with off-white ridges; 206–*245*–303μ in diameter, 7 spores measured; with broad muri of medium height (Fig. 26–27).—There is wide variation in spore size and frequently three small spores and one large spore in each sporangium. There is one basal megasporangium per strobilus.

Microspores. Light Buff (sand); 22–*31*–35μ in diameter, 20 spores measured; spines with rather wide, crowded bases.

Selaginella maginata (Humb. & Bonpl.) Spring.

Megaspores. Light Salmon-Orange; 458μ in diameter, one spore measured; with high, very slender muri.—The spore walls are very thin and break easily,

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FIGURES 52–66.—Microspores of *Selaginella.* — 52. *S. novoleonensis,* tetrad, × 395. — 53–54. *S. schiedeana,* × 580.—53. Distal face.—54. Proximal face. — 55–56. *S. schaffneri,* × 580.—55. Distal face.—56. Proximal face. — 57 59. *S. delicatissima,* × 580.—57, 59. Distal face.—58. Proximal face. — 60. Presumed hybrid, × 580. — 61–62. *S. silvestris* × 580.—61. Distal face.—62. Proximal face. — 63 64. *S. articulata,* × 660.—63. Distal face.—64. Proximal face. — 65–66. *S. horizontalis,* × 660.—65. Distal face.—66. Proximal face.

thus only one measurement was possible. There is one basal megasporangium per strobilus.

Microspores. Capucine Buff (beige); 20–26–34μ in diameter, 20 spores measured; projections sparse, ranging from long papillae to broad, blunt spines (Fig. 50–51).

Selaginella sertata Spring.

Megaspores. Cream Color with white ridges; 382–494–526μ in diameter, 10 spores measured; with high, narrow muri, aeroles crossed by minor ridges; one basal megasporangium per strobilus (Fig. 21–22).

Microspores. Light Ochraceous Buff (beige); 22–25–29μ in diameter, 20 spores measured; spines long on the distal face and very short on the proximal face.

Selaginella silvestris Aspl.

Megaspores. None found.

Microspores. Pale Ochraceous Buff (beige); 28–40–47μ in diameter, 20 spores measured; spines limited to the distal face and more distantly spaced than in other species of the articulate group; spines variable in size from spore to spore (Fig. 61–62).

Selaginella galeottii Spring.

Megaspores. Buckthorn Brown with off-white ridges; 382–443–494μ in diameter, 8 spores measured; with broad muri of medium height; one basal megasporangium per strobilus.

Microspores. Pale Yellow-Orange (beige); 25–31–39μ in diameter, 20 spores measured; spines on both faces.

Selaginella intacta Baker.

Megaspores. Light Buff (sand) with off-white ridges; 347–437–526μ in diameter, 10 spores measured; with low, broad muri, minute papillae in the areoles; generally two large and two small spores in each sporangium (Fig. 23–24).—The strobili are wholly microsporangiate, have a basal megasporangium and no other sporangia above, or have a basal megasporangium and a few microsporangia at the top of the strobilus.

Microspores. Cinnamon Buff (tan); 22–30–36μ in diameter, 20 spores measured; with spines.

Selaginella horizontalis (Presl) Spring.

Megaspores. Cream Color (off-white); 357–377–437μ in diameter, 10 spores measured; narrow muri of medium height; one basal megasporangium with 3 large and 1 small spore per strobilus.

Microspores. Pale Ochraceous Buff (beige); 24–28–31μ in diameter, 20 spores measured; with spines (Fig. 65–66).

Selaginella eurynota A. Braun.

Megaspores. Cinnamon (brown), muri almost white; 448–479–510μ in diameter, 10 spores measured; with high, narrow muri.—There is one basal mega-

sporangium per strobilus and tendency toward inequality of spore size in any one sporangium.

Microspores. Pale Yellow-Orange (beige); 22–29–36μ in diameter, 20 spores measured; spines quite crowded.

Selaginella schizobasis Baker.

Megaspores. Light Pinkish Cinnamon (pale brown) with white ridges; 301–372–523μ in diameter, 5 spores measured; with broad muri of medium height; some sporangia with one larger and some with two larger spores.—There is one basal megasporangium per strobilus.

Microspores. Pale Orange-Yellow (beige); 18–30–42μ in diameter, 20 spores measured; with spines.

Selaginella kunzeana A. Braun.

Megaspores. White; 382–443–464μ in diameter, 10 spores measured; ridges of medium height and width, areoles with many papillae.—There is one basal megasporangium per strobilus.

Microspores. Capucine Buff (tan); 26–31–34μ in diameter, 20 spores measured; with spines.

Key to Heterophyllous Selaginellae

1. Microspores not spiny, with blunt projections, ridges or no ornamentation; orange in color; megasporangia more than one per strobilus or, if only one, not located at base of strobilus (Non-articulate group) 2
   2. Microspores shed in tetrads encased in a common sculptured wall ..... *S. lepidophylla, S. novoleonensis*
   2. Microspores generally shed separately, if in tetrads never encased in a common wall 3
      3. Microspores with projections other than elongate ridges 4
         4. Microspores with capitate projections 5
            5. Megaspores averaging 200–290μ (188–291μ) in diameter; papillae of microspores usually long and slender 6
               6. Megaspores averaging 200–240μ (188 255μ) in diameter, little breakage in preparation 7
                  7. Microspores averaging 19μ (18 21μ) in diameter, often shed in tetrads; megasporangia very few ..... *S. novae-hollandiae*
                  7. Microspores averaging 25–30μ (22–31μ) in diameter, shed individually; megasporangia numerous 8
                     8. Megasporangia located in the lower half of the strobili; microspores with slender papillae ..... *Selaginella* unknown sp. 1, *S.* unknown sp. 2, *S. flagellata*
                     8. Megasporangia arranged in two longitudinal rows; microspores with stout papillae often with divided heads. *S. cladorrhizans*
               6. Megaspores averaging 275μ (255–291μ) in diameter, much breakage in preparation ..... *S. tarapotensis*
            5. Megaspores averaging 315 420μ (300-448μ) in diameter; papillae of microspores usually short and stout 9
               9. Megaspores averaging 420μ (387 448μ) in diameter; microspores averaging 22μ (21–24μ) in diameter; megasporangia basal ..... *S. pallescens*
               9. Megaspores averaging 315–350μ (300–398μ) in diameter; microspores averaging 30 36μ (26–40μ) in diameter; megasporangia not basal 10

10. Megasporangia in two longitudinal rows; papillae of microspores with massive, round heads ..... *S. bombycina*
10. Megasporangia in no constant arrangement; papillae of microspore heads not massive 11
11. Papillae of microspores often with split heads.. *S. pulcherrima*
11. Papillae of microspores all with round heads.. *S. microdendron*

4. Microspores with non-capitate papillae 12
12. Microspores averaging 35–50μ (29–56μ) in diameter 13
13. Megaspores and microspores with similar papillate markings; megaspores averaging 475μ (443–496μ) in diameter. *S. delicatissima*
13. Megaspores with ridges unlike the papillae of the microspores; megaspores averaging not more than 425μ (219–469μ) in diameter 14
14. Megaspores averaging 400μ (331–469μ) in diameter; usually 3 large and 1 small spore in each megasporangium; microspore papillae irregular in size ..... *S. schiedeana*
14. Megaspores averaging 225μ (219–240μ) in diameter; all spores in each megasporangium of equal size; microspore papillae regular in size ..... *S. ovifolia*

12. Microspores averaging 20–25μ (19–29μ) in diameter 15
15. Microsporangia few, scattered in the strobili ..... *S. anceps, S. mollis*
15. Microsporangia equal to or exceeding in number the megasporangia which are either basal or in two longitudinal rows 16
16. Megasporangia basal; megaspores averaging 290–375μ (245–484μ) in diameter 17
17. Megaspores averaging 290μ (245–321μ) in diameter. *S. illecebrosa*
17. Megaspores averaging 375μ (306–484μ) in diameter. *S. estrellensis*
16. Megasporangia in two longitudinal rows; megaspores averaging 225–235μ (204–296μ) in diameter ..... *S. haematodes, S. umbrosa*

3. Microspores with elongate ridges, heavy ridge-like papillae, or with no markings at all 18
18. Microspores with no markings or with very thin walls covered with a granular material 19
19. Microspores with no markings ..... *S. revoluta*
19. Microspores with thin walls covered with a granular material ... *S. porphyrospora*

18. Microspores with ridges 20
20. Microspores with ridges covering most of the surface, ridges very low, up to 8μ wide; microspores averaging 56μ (47–63μ) in diameter ..... *S. schaffneri*
20. Microspores with ridges not covering most of surface, ridges with distinguishable height, not more than 5μ wide; microspores averaging 23–28μ (20–36μ) in diameter 21
21. Microspores with heavy, ridge-like, amorphous papillae 22
22. Megasporangia very few, often only one per strobilus; papillae of microspores ridge-like only at the equator..... *S. reflexa*
22. Megasporangia numerous; papillae of microspores ridge-like on the distal face as well as at equator 23
23. Megasporangia basal ..... *S. stenophylla*
23. Megasporangia in two longitudinal rows ..... *S. lychnuchus*

21. Microspores with thin precise ridges or very faint ones, never massive 24
24. Microspores with faint amorphous ridges 25
25. Megaspores with papillae on the proximal face .. *S. oaxacana*
25. Megaspores without papillae on the proximal face. *S. martensii*

24. Microspores with precisely marked ridges up to 3μ wide usually with distinguishable height, especially at the equa-

tor of the spore 26
26. Microspore ridges never extended to form blunt spine-like projections; microspores often shed in tetrads. . *S. idiospora*
26. Microspore ridges often elongated into blunt spine-like projections; microspores not shed in tetrads 27
27. Megaspores averaging 275μ (240–316μ) in diameter; megasporangia in two longitudinal rows ... *S. hoffmannii*
27. Megaspores averaging 375μ (316–458μ) in diameter; megasporangia basal ..... *S. guatemalensis, S. huehuetenangensis*

1. Microspores with sharp-pointed spines (except *S. exaltata* and *S. marginata*); microspores tan (except pale orange-tan in *S. marginata*); megasporangium one, basal; strobilus usually conspicuously swollen at base; megaspores with high, definite muri (Articulate group) 28
28. Microspores lacking sharp projections 29
29. Microspores with slender blunt projections; megaspores averaging 1,115μ (1,058–1,176μ) in diameter ..... *S. exaltata*
29. Microspores with wide flattened projections; megaspores averaging 450μ (–458μ) in diameter ..... *S. marginata*
28. Microspores with sharp-pointed spines 30
30. Microspores averaging 40μ (28–47μ) in diameter; microspore spines few ..... *S. silvestris*
30. Microspores averaging 25–31μ (18–42μ) in diameter; spines numerous 31
31. Three large and 1 small or 2 large and 2 small spores in each megasporangium 32
32. Megaspores averaging 250μ (206–303μ) in diameter ..... *S. arthritica*
32. Megaspores averaging 375 480μ (301–526μ) in diameter 33
33. Megaspores averaging 370 380μ (301–523μ) in diameter 34
34. Megaspores pale brown with white ridges; megaspore muri up to 15μ wide ..... *S. schizobasis*
34. Megaspores off-white; megaspore muri up to 5μ wide .... *S. horizontalis*
33. Megaspores averaging 435–480μ (347–510μ) in diameter 35
35. Strobili often varying from the one basal megasporangium pattern ..... *S. intacta*
35. Strobili always with one basal megasporangium ..... *S. eurynota*
31. All spores in each megasporangium of equal size 36
36. Megaspores averaging 570μ (529 588μ) in diameter ..... *S. articulata*
36. Megaspores averaging 440–500μ (382–526μ) in diameter 37
37. Megaspores with muri up to 25μ wide; megaspores brown with white muri ..... *S. galeottii*
37. Megaspores with muri 10–15μ wide; megaspores white or cream color with off-white muri 38
38. Megaspores cream with white muri; megaspore areoles crossed by minor ridges ..... *S. sertata*
38. Megaspores white; megaspore areoles with many minute papillae ..... *S. kunzeana*

Observations

Spore Color. The muri and ridges of megaspores are often a different color than the spore wall, so it is often difficult to judge the color of the spores. There also seems to be a tendency toward loss of color or change in color with age. One specimen was annotated as having yellow spores, but only brown ones could be found. The color of the megaspores is so variable as to be of little use in segregating groups. None of the species groups in Alston's key (1955) is characterized by any one color.

Microspore color, on the other hand, shows a nearly perfect correlation with stem articulation. The microspores of the non-articulate species are all some shade of orange; those of the articulate species are tan.

Spore Size. Megaspore size is extremely diverse, ranging from 224μ in *S. flagellata* to 1.2 mm in *S. exaltata.* However, size gives little indication of relationship. With the exception of *S. arthritica,* megaspores of the articulate species are large, but several non-articulate species also have large spores.

Within a single megasporangium the spore size may vary. In some species there are regularly one large and three small spores, and in other species regularly two large and two small spores. Certain species may vary as to the spore size relationship in different sporangia. This variability is found in both articulate and non-articulate species. A more detailed investigation is needed both on megaspore ontogeny and on viability of the different-sized spores. There may be a trend toward a single functional megaspore.

Microspore sizes are mostly between 20 and 30μ, although a few species have much larger spores. *Selaginella schaffneri,* for example, has microspores 56μ in diameter. Microspore size, however, is apparently not correlated with taxonomic groupings, and the larger microspores may be a result of polyploidy.

Spore Wall Ornamentation. The wall ornamentation of the megaspores is not easily characterized; however, some types can be recognized. The spores of the articulate species generally have higher muri than those of the non-articulate species. Within the articulate species the spores may be further divided on the basis of height and width of the muri. High, narrow muri are found in *S. exaltata* (Fig. 28–29) and *S. sertata* (Fig. 21–22). Low, broad muri occur on the spores of *S. articulata* (Fig. 30–31).

The megaspores of the non-articulate species generally have low ridges (Fig. 11, 17). Correlated with the lower ridges is a lesser degree of ornamentation on the proximal face. There are, however, a few species of the non-articulate group, such as *S. mollis* (Fig. 15–16), which have spores with narrow muri similar to those of the articulate species. Most commonly the megaspores of the non-articulate group have ridges which vary from low, broad ones which are nearly free of anastomoses in *S. tarapotensis* (Fig. 17–18) to very low ones which run together freely but still leave many free ends, as in *S. pallescens* (Fig. 7–8).

These spores have different markings on their proximal faces ranging from pointed peaks on the low ridges in *S. guatemalensis* (Fig. 2) to low papillae in *S. oaxacana* (Fig. 12). This papillosity is carried to the extreme in *S. delicatissima* (Fig. 19–20) in which papillae are the only markings on all faces. This species is the only one studied in which megaspores and microspores look alike.

The ornamentation of the microspores also reflects the distinctness of the articulate group and the non-articulate group. The articulate species generally have sharp-pointed spines (Fig. 61–66), which no members of the non-articulate group have. The only two articulate species that lack spines are *S. marginata* (Fig. 50–51), which has long, broad projections, and *S. exaltata* (Fig. 40–41), which has has long, somewhat capitate papillae closely resembling those found in many non-articulate species (Fig. 38–39).

Papillae seem to be the basic type of ornamentation on the microspores of the non-articulate species; there are several variations of this general shape. *Selaginella umbrosa* (Fig. 32–33) has representative papillose microspores. *Selaginella delicatissima* (Fig. 57–58) has very small papillae which cover all faces, but the papillae may coalesce to form short ridges (Fig. 59). The papillae are short and massive in *S. ovifolia* (Fig. 46–47) and *S. reflexa* (Fig. 48–49).

Capitate papillae reach two extremes. *Selaginella tarapotensis* (Fig. 36–37), for example, has short, stout projections. *Selaginella flagellata* (Fig. 38–39), on the other hand, has long, narrow, capitate projections.

In some species microspore ornamentation is in the form of ridges. Ridges are very short and indistinct in *S. oaxacana,* whereas in other species such as *S. idiospora* (Fig. 42–43), the ridges are definite but not anastomosing. The ridges are long and anastomosing, ending in spine-like projections in *S. guatemalensis* (Fig. 44–45) and *S. huehuetenangensis.* The wall of *S. schaffneri* (Fig. 55–56) is distinctive in being extremely thick with scattered depressions. This pattern may possibly be formed from fusion of broad papillae or ridges.

Selaginella revoluta (Fig. 34–35) is the only species with microspores which do not have any ornamentation at all. The spores are assumed to be mature since they were all free of tetrads.

Perhaps the most distinctive microspore specialization is found in those species characterized by the plants curling into a ball in dry seasons. These species represented by *S. novoleonensis* (Fig. 52) and *S. lepidophylla,* shed their microspores in tetrads. Apparently the heavy outer wall is common to the entire tetrad and is ornamented by several ridges. Furthermore, there seems to be a tendency among many of the other non-articulate species to shed at least some of their microspores in tetrads.

Sporangial Arrangement. Sporangial arrangement patterns in 42 species were apparent. Once again the articulate species display a common pattern — a single basal megasporangium with many microsporangia above it. *Selaginella intacta* of the articulate group has some strobili with two megasporangia at the base.

Among the non-articulate species only *S. schaffneri* and *S. schiedeana* have a single basal megasporangium. Other patterns found include the lower half of the strobilus being megasporangiate and the upper half microsporangiate *(S. delicatissima),* two rows of megasporangia and two of microsporangia *(S. bombycina),* a very few megasporangia scattered in the strobilus *(S. lepidophylla),* and a very few microsporangia in the strobilus *(S. anceps)* with *S. revoluta* being the extreme with one microsporangium at the tip of the strobilus.

Conclusions

The spores of *Selaginella* are of considerable taxonomic value. Alston (1955) used them in his key to separate some species, but he did not use them in separating larger groups of species. The present study shows that certain spore characters can be useful in defining these groups.

The most obvious separation based on spore characters is between the articulate and non-articulate species. Four spore characters — microspore color and

ornamentation, megaspore ornamentation and size — plus sporangial arrangement indicate the distinctness of the two groups. The spores of the articulate species are not as diverse as those of the non-articulate group; therefore, the latter group can more easily be further divided on the basis of spore characters.

Within the non-articulate group the *S. lepidophylla* group seems to be distinct based on spore characters as well as other morphological features. The microspores shed in tetrads encased in heavy common walls in this group is unique among the species studied.

Other groupings in Alston's key (1955) were not upheld as well by spore characters. However, some species, such as *S. guatemalensis* and *S. huehuetenangensis,* which occur together in the key, have similar spores. More detailed studies may help define more groups based on the spore characters within the heterophyllous *Selaginellae.*

Several additional problems which could be investigated with profit presented themselves in the course of this work. Studies of sporangial arrangement, spore ontogeny, hybridization and polyploidy, and spore ornamentation on a worldwide basis would prove to be of developmental, morphological, and taxonomic interest.

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THE OZARK FLORA—SOME COLLECTIONS OF NOTE

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Abstract

Recent collecting has produced eight major range extensions or other unusual plants for the Ozark flora.

A newcomer to the Missouri area last summer, 1969, I made some 500 vascular plant collections with a view to acquainting myself with the plants growing in the Ozarks and the Mississippi River Valley. Most collecting was in the St. Francois Mountain area but one foray was made to the "bootheel" counties of southeastern Missouri and into adjacent Arkansas; and a number of trips included Illinois counties near St. Louis. Material of all collections is lodged with the Missouri Botanical Garden (MO), and duplicates were distributed to other institutions as indicated.

The following list of major range extensions or unusual plants does not include all new county records which may have been taken. In spite of the large collections made in the past by such botanists as Bush, Palmer and Steyermark and the very fine presentation of results in Steyermark's (1963) *Flora of Missouri,* there is still a great deal of work to be done before this area can be said to have a well known flora. That such indiscriminate collecting as my own last summer could produce the following list is evidence of the need for much more field work.

ANEMONELLA THALICTROIDES (L.) Spach f. FAVILLIANA Bergs. *in* Fass. *D'Arcy 3130* (MO).

Forma *favilliana* is "a beautiful form of Rue Anemone, resembling a miniature tuberous begonia, marigold, or zinnia in the buttonlike condensed flowers" (Steyermark, 1963). This pretty little variant was found growing at the wet edge of a sloping oak woods by a secondary road about one mile north of Bonne Terre, St. Francois County, Missouri. Only one plant was seen growing with the usual understory sprinkling of the typical variety, and in fact my collection is mixed with plants of the typical form.

Formerly known in the wild in Missouri only from Putnam County in the extreme north and from Carter County in the south of the state, my collection provides an intermediate station. This distribution does not suggest any former wide-spread distribution or relict status but seems rather to be the result of the rare recurrence of a mutant gene. Because they are apparently sterile, new occurrences of the form are unlikely to build up significant populations, although Steyermark (1963) mentions propagating it by dividing the roots.

Forma *favilliana* was first described from Wisconsin in 1946. Bernard Boivin (1957) provided the alternative name: *Thalictrum thalictroides* (L.) Boiv. f. *favilliana* (Bergs. *in* Fass.) Boiv.

RANUNCULUS ARVENSIS L. *D'Arcy 3181* (MO, BSI, GH, UMO).

This very showy yellow buttercup was taken on the north side of Huffman, Arkansas. The flat, low fields in this area were host to frequent rather large patches of the weed. Huffman is in the extreme northeastern corner of Mississippi County, Arkansas, and is less than five miles from the southeastern corner of the Missouri bootheel. *Ranunculus arvensis* is a likely candidate for colonization of any of the low areas bordering the Mississippi River in this latitude. In 1959, Muelenbach found it on the north side of the city of St. Louis, not in St. Louis County as indicated by Steyermark in his *Flora.*

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Ann. Missouri Bot. Gard. 56: 465–467. 1969.

Draba aprica Beadle *ex* Small. *D'Arcy* 3257 (MO, GH, LE, UMO); *Palmer* 5500 (MO).

While checking the identification of my specimen, I came across the Palmer collection, which was taken 5 May, 1914, from "Dry rocky ground—high hills, Noel, McDonald County, Missouri." This is two hundred miles to the southeast of the Reynolds County report of Steyermark (1963) and is about seventy-five miles north of the southeastern Oklahoma station reported by Rollins (1961). The Palmer collection consists of ten plants which I take to be the same taxonomic entity. It was unnamed as to species, but on a second label Palmer indicated he had something unusual: "Note sparingly dentate stem leaves, short branches with fascicle-like pods and *pubescent fruits.*"

Draba aprica has been a puzzle to other botanists besides Palmer. Schulz (1927), Nuttall (Torrey & Gray,1838), and Hitchcock (1941) accepted this plant as a variety (var. *fastigiata* Nutt. *ex* T. & G.) of *Draba brachycarpa* Nutt. *ex* T. & G., which is very similar. Small (1913), Fernwald (1934), Rollins (1961), and Steyermark (1940, 1963) held it to be a distinct species, with Rollins (1961) providing the most recent and emphatic argument. Hitchcock discussed the Palmer specimen (*Palmer 5500*, POM), suggesting that Missouri plants and those reported earlier from Georgia originated independently and that they might be tetraploids. There has also been a question as to the correct origin of Nuttall's plants which form the type of var. *fastigiata.* Steyermark (1959) shows the route of Nuttall's travels passing about midway between the localities for the Palmer collection and the Oklahoma collection reported by Rollins, so the Arkansas location indicated by Nuttall is certainly plausible.

My collection is from a steep oak-pine slope just east of the St. Francois River in Madison County, Missouri. This isolated hill is only about two miles north of the St. Francois Shuttins where Steyermark collected *D. aprica* in 1930. Apparently the Madison County population of pubescent fruited plants is persistent, whatever taxonomic rank is applied.

Cornus florida L. f. rubra (Weston) Palmer & Steyerm. *D'Arcy* 3235 (MO, A, BSI, SIU, UAC).

Growing in a well-shaded location on a south-facing slope of very fine-grained red granite and in an oak-pine woods with a fine understory of dogwood and sassafras about one mile west of Mill Creek, Madison County, Missouri, is a small dogwood tree which bears bright pink flowers. Not only were the bracts pink, but they were striped with lighter and darker shades of pink and crimson. Examination of neighboring trees showed that they too had an element of pink in the bracts, but the admixture of color was so small that they might have passed as ordinary white dogwoods. Apparently the gene or genes causing the coloration occurs with varying effect throughout this small population. Steyermark (1963) states that the pink flowered dogwood is rarely encountered in the wild. In this case, the woods where it occurred seemed to have been undisturbed for many years.

Desmodium viridiflorum (L.) DC. *D'Arcy* 3779 (MO, 3 sheets).

This tick clover, which has tomentose petiolules and small purple flowers which fade teal blue, has leaflets of quite variable size, the medians ranging from less than 4 cm to over 11 cm long on neighboring plants. Steyermark (1963) questioned the validity of *D. nuttallii* (Schindl.) Schub. as distinct from *D. viridiflorum* but deferred to Isely (1955) and included it as a separate species.

From my collection it is not apparent which of the two species was present. One element clearly conforms to *D. nuttallii* as delineated by Isely (1953; 1955), while the others either conform to *D. viridiflorum* or lack fruits adequate for certain determination. Except for leaf size, the population looked rather uniform in the field, but it may have been a mixed population.

This colony was under shade on a red granite hillside about one mile west of Mill Creek, Madison County. It was only a few feet from the site of the pink dogwood described above and just above the road where the *Artemisia ludoviciana* patch (below) was found. This hill is a southeastern extension of Devon Mountain. Treated as *D. viridiflorum sensu stricto,* this collection is a considerable northward extension of range; while as *D. nuttallii* it represents a new county record on the northern edge of the Missouri range.

Physostegia formosior Lunell. *D'Arcy 3804* (MO, DAO, FSU, GH, LE, SIU, UMO).

A showy if sprawling mint, this plant was scattered along the upper tributaries of Crane Pond Creek in Iron County where it was competing with *Hamamelis vernalis* for footholds

on the small gravel bars and banks. Most plants were tilted to one side as if the streams had just pushed them over, and that was likely the case. Although he does not refer to it in his text, Steyermark (1963) shows a dot on his map indicating this species for Iron County. It is difficult to believe, however, that this is the only county in the St. Francois Mountain area where this species occurs.

KRIGIA OCCIDENTALIS Nutt. *D'Arcy & Porter* 3328 (MO).

"In sandy soil under oaks & pines above large spring, Pickle Springs, Ste. Genevieve County" is the label information on the plant I collected with Dr. D. M. Porter on 25 May, 1969. This species is comparable in size with *K. virginica* (L.) Willd. which occurs in the same region, but it has fewer involucral bracts.

The Pickle Springs locality is at the eastern edge of the Cambrian La Motte sandstone formation and is the westernmost station for a number of Appalachian and other eastern plants, especially bryophytes. In this case, however, it is the easternmost location for a southwestern species centered in Texas and Oklahoma and represents an eastward range extension of about two hundred miles.

ARTEMISIA LUDOVICIANA Nutt. *D'Arcy* 3772 (MO, DAO, GH, ISC, LE, SIU, UMO).

A large white patch of roadside weeds provided the specimens of this species. On the lower side of State Road T, about one mile west of Mill Creek in Madison County, as it winds up around a red granite hill was a weed patch containing flourishing populations of *Lespedeza striata, Ambrosia bidentata* and *Croton monanthogynus*. The *Ambrosia* was in several pure colonies about 1 m across. The red granite hill is the same that provided the specimens of *Cornus florida* and *Desmodium viridiflorum* noted above. This location is a significant extension of present known range of *A. ludoviciana* in an easterly direction, although Nuttall (1818) reported it from "the banks of the Mississippi, near St. Louis; also on the alluvial plains of Missouri."

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NOTES

ADDITIONAL TYPE MATERIAL OF *BOUVARDIA* (RUBIACEAE)

We have recently discovered that type specimens to which eight specific epithets of *Bouvardia* apply are extant in the Herbarium of Martin Luther University (HAL), Halle, German Democratic Republic. The majority were collected by C. J. W. Schiede and subsequently described by D. F. L. von Schlechtendal in his early monograph of the genus (Linnaea 26: 43–126. 1854). We formerly thought these types to have been deposited in Berlin (B) and destroyed. They were noted as B† (Berlin destroyed) in a recent revision (Blackwell, Ann. Missouri Bot. Gard. 55: 1–30. 1968). Careful study of this material has revealed no need to overturn names presently considered correct. However, the following alterations in typification and synonymy should be noted.

The types of *Bouvardia microphylla* Schlecht., *Schiede* 563 (HAL 21736), and *B. viperalis* Schlecht., *Schiede 1226* (HAL 21742), clearly implicate both as synonyms of *B. ternifolia* (Cav.) Schlecht. As such, these names should be removed from the list of doubtful or excluded taxa. *Bouvardia tenuiflora* Schlecht., type: *Schlechtendal s.n.* (HAL 24687), is confirmed as a synonym of *B. ternifolia,* being formerly so placed on the basis of circumscription alone. Also on the basis of circumscription, *B. schiedeana* Schlecht. was included in the synonymy of *B. multiflora* (Cav.) Schultes & Schultes f. However, the type, *Schiede s.n.* (HAL 24688), is a problematical specimen, resembling both *B. multiflora* and *B. laevis* Martens & Gal. *Bouvardia multiflora* and *B. laevis* are closely related species and intermediates are encountered (Blackwell, *loc. cit.* 7). After examining the type specimen in question, we believe its morphology actually falls within the limits of variation of *B. laevis* and that the name *B. schiedeana* is best removed to the synonymy of this species. Though lacking complete flowers, the type of *B. myrtifolia* Schlecht., *Schiede* 554 (HAL 21737), substantiates its inclusion in the synonymy of *B. chrysantha* Mart. *Bouvardia houtteana* Schlecht. *ex* Planch., type: *van Houtte s.n.* (HAL 24693), is evidently a horticultural form of *B. ternifolia* and may thus be retained in its synonymy.

Neotypes designated for the correct names *B. viminalis* Schlecht. and *B. rosea* Schlecht. are now superseded by the rediscovered original material. *Schiede* 557 (HAL 21741), Mexico, *s. loc.*, may be regarded as the holotype of *B. viminalis.* Lectotypification of *B. rosea* is appropriate since three collections, *Schiede* 556, 558 and 576 are syntypic. *Schiede* 576 (HAL 21738), Mexico, near San José del Oro, cold region, is here selected as lectotype as it is the best specimen.

It is of interest to note that the numbers of the Schiede collections, *e.g. Schiede* 557, are not actually Schiede's collection numbers. They are herbarium

numbers added to the Schiede collections by C. Ehrenberg who worked on the collections after Schiede's death (personal communication from Dr. Klaus Werner, Curator at Halle).

The original description of *Bouvardia chrysantha* Martius, in *Delectus Seminum in Horto R. Botanico Monacensi Collectorum Anno 1848* (apparently unpaginated), has now been seen and corroborates selection of this name as the correct one.

The herbarium at Halle is gratefully acknowledged for the loan of specimens of *Bouvardia.* — *Will H. Blackwell, Jr., Department of Botany, Miami University, Oxford, Ohio* and *Marshall C. Johnston, Department of Botany, The University of Texas at Austin.*

A NEW SPECIES OF *SCAEVOLA* (GOODENIACEAE) FROM TAHITI

The novelty presented here is of interest because it fills a gap in the geographical range of the purple-fruited montane species of *Scaevola* which range from New Caledonia to Hawaii. These belong to sect. *Scaevola* (formerly sect. *Sarcocarpaea*) and are discussed in a preceding paper (Ann. Missouri Bot. Gard. 56: 358–390. 1969).

Scaevola tahitensis Carlquist, sp. nov.

Frutex erectus 1–2 m altus ramulis teretibus validus novellis dense breviter cinerascenti-tomentosis adultis tomentosis in axillis foliroum barbatis obtectis superne cicatricibus foliorum delapsorum ± dense notatis. Folia ad ramulorum apices conferta subcoriacea elliptica vel oblanceolato-elliptica, apice acuta basin versus in petiolum brevissimum validum latiusculum angustata, margine integra rarissme obscure crenata, 4–11 plerumque 8 cm longa, 1–2.5 plerumque 2.2 cm lata, supra dense cinerascenti-tomentosi, subtus dense cinerascenti-tomentosi, costa media atque nervis primaris 6–12 supra paullum impressis subtus distincte prominentibus percursa. Flores in cymis axillaribus dispositi. Flores ignotis. Fructus ovoideus ca. 4 mm metiens.

Erect, often little-branched *shrub,* 1–2 m tall, branches terete, densely short-tomentose, with barbate accumulations of hairs in leaf axils. *Stem* with leaves grouped in dense rosettes at tips of branches, leaf scars also conspicuous at tips of shoots. *Leaves* subcoriaceous, elliptical or oblanceolate-elliptical, tips acute, narrowed below into a very short petiole (or petiole absent); margins entire or very rarely slightly crenate. Leaves 4–11 (mostly 8) cm long, 1–2.5 (mostly 2.2) cm wide, densely short-tomentose above and below, the midrib and 6–12 primary nerves obvious above and, less distinctly, visible below also. *Inflorescence* an axillary cyme. *Flowers* unknown, only a few weathered fruits, these about 4 mm

long, seen in the field (these were observed at the time of collecting but have now been lost).

Type and only collection: TAHITI: With *Alstonia, Ilex,* in *Dicranopteris* mats on rocky ridge above Rocher du Diable, ca. 4,000 feet elevation, on Fare Rau Ape-Aorai Trail, Mt. Aorai. June 15, 1962. *S. Carlquist 654* (RSA).

The widespread pan-Pacific beach *Scaevola, S. taccada,* is present on many islands of southeastern Polynesia. There has been no report, however, of any purple-fruited montane *Scaevola* from any of the archipelagoes between Samoa and the Marquesas. A *Scaevola* would be expected on the mountains of Tahiti (or others of the Society Islands), for the same ecological conditions that prevail on the other high Pacific islands where *Scaevola* occurs are present on Tahiti also. *Scaevola tahitensis* belongs to the series of species that begins with *S. montana* and allied species in New Caledonia and continues with *S. floribunda* (Fiji), *S. nubigena* (Samoa), *S. subcapitata* and *S. marquesensis* (Marquesas), and *S. gaudichaudiana, S. chamissoniana,* and *S. mollis* (Hawaiian Islands).

Scaevola tahitensis can be distinguished very easily from other species in this series by vegetative characteristics alone. Both upper and lower leaf surfaces are densely tomentose or velutinous, and the leaf margins are virtually entire, with only the slightest evidence of teeth. The species that most closely approaches *S. tahitensis* is perhaps *S. floribunda,* in which trichomes are much shorter and less dense than those of *S. tahitensis;* they are, in fact, difficult to detect without considerable magnification. The markedly crenate or undulate margins of leaves of *S. floribunda,* with exserted, closely-spaced teeth, are unlike those of *S. tahitensis. Scaevola marquesensis* has revolute margins with less prominent but more closely spaced teeth than those of *S. floribunda.* Leaves of *S. marquesensis* are glabrous or nearly so at maturity. *Scaevola subcapitata* is very similar to *S. marquesensis,* and very likely one of the two species should be regarded as a synonym. *Scaevola nubigena* has prominent, widely spaced teeth, along undulate margins that are revolute, and it has glabrous leaf surfaces.

In addition, *Scaevola floribunda* differs in leaf shape—its leaves are long and markedly petiolate. Leaves of *S. marquesensis* and *S. subcapitata* are shorter and broader (in proportion to their length) than those of *S. tahitensis* and have obtuse apices.

Because *Scaevola tahitensis* is a very distinctive species, I am describing it despite the scantiness of the material. Hopefully other collectors will discover this plant in flower. It might be found in flower during the southern hemisphere summer (November to January). Data on wood anatomy of *S. tahitensis* are offered in a preceding paper (Ann. Missouri Bot. Gard. 56: 358–390. 1969).

Scaevola tahitensis was collected during travel financed by a grant from the National Science Foundation, NSFG-23396.—*Sherwin Carlquist, Claremont Graduate School, Rancho Santa Ana Botanic Garden, Claremont, California.*

CHROMOSOME NUMBERS OF PHANEROGAMS. 3.[1]

Chromosome numbers of phanerogams are reported below together with voucher data and herbaria where collections are deposited. Unless indicated the chromosome records are based on the study of one plant. Haploid counts are from pollen mother cells, and diploid counts are from root tips unless otherwise indicated. An asterisk indicates that one or more permanent slides are available at the Missouri Botanical Garden Herbarium.

The authors responsible for counts are listed alphabetically. Citation should have the form: Doe, J. 1969. *In* Chromosome numbers of phanerogams. 3. Ann. Missouri Bot. Gard. 56:

Counts by W. G. D'Arcy, Missouri Botanical Garden.

SOLANACEAE

Physalis peruviana L. n = 24, meiosis regular. PORTUGAL. Seed from the Jardim Botânico, Coimbra, grown at Missouri Botanical Garden, *D'Arcy 3116* (DAO, FSU, MO).

Solanum carolinense L. n = 12, meiosis regular. ILLINOIS. CLINTON COUNTY: Along U.S. highway 50, about 14 mi. W of Carlyle, *D'Arcy 3424* (MO). MARION COUNTY: Sandoval, *D'Arcy 3429* (MO); along U.S. highway 50, about 4 mi. E of Sandoval, *D'Arcy 3431* (MO); W side of Salem, *D'Arcy 3438* (MO).

Solanum carolinense var. *floridanum* A. Gray. n = 12, meiosis regular. FLORIDA. CLAY COUNTY: W side of Doctors Inlet, *D'Arcy 3501* (FLAS).

Solanum dimidiatum Raf. n = 36 ± 1, meiosis regular. FLORIDA. ALACHUA COUNTY: W of Gainesville, along dirt road between Fla. highways 24 and 26, 1 mi. W of U.S. highway 75, *D'Arcy 1587* (FLAS, MO). GILCHRIST COUNTY: About 2 mi. W of Bell, along Fla. highway 341, *D'Arcy 2477* (FLAS, MO). In both colonies, proliferation was mainly if not entirely by underground stolons. In the Alachua County population little or no fruit set and matured. Fruits in the Gilchrist County population contained fewer than eight normal-looking seeds and many aborted ovules appearing like specks of pepper on the inside of the carpels. This is one of the first reports of polyploidy in *Solanum* subgenus *Stelatipilum* Seithe.

Solanum diphyllum L. n = 12, meiosis regular. FLORIDA. ALACHUA COUNTY: University of Florida campus, Gainesville, *D'Arcy 3500* (FLAS).

Solanum lanceaefolium Jacq. n = 12, meiosis regular. VIRGIN ISLANDS. TORTOLA: Sage Mountain Ridge, seed from *D'Arcy 2070* (FLAS), grown at the Missouri Botanical Garden, *D'Arcy 2070B* (MO).

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[1] Previous numbers in this series have appeared in Ann. Missouri Bot. Gard. 53: 100–103, 1966; Ann. Missouri Bot. Gard. 54: 178–181, 1967.

Solanum persicaefolium Dun. n = 12, meiosis regular. PUERTO RICO. Seed collected by Richard J. Wagner, grown at the Missouri Botanical Garden, *D'Arcy 3896* (MO).

Solanum torvum Sw. n = 12, meiosis regular. COSTA RICA. Seed accidentally introduced and growing in greenhouse, University of Florida, Gainesville, *D'Arcy s.n.* (FLAS).

Solanum tridynamum var. *anoplocladum* Dun. 2n = 24. FLORIDA. Seed from Tom & Bob's Nursery, 9550 SW 67th Avenue, Miami, grown at Missouri Botanical Garden, *D'Arcy 3901* (FTG, MO). This plant has been known as *S. amazonium* Ker-Gawl. (Bot. Reg. t. *71*, 1815). The microfiche edition of the *Prodromus* herbarium of DeCandolle (G-DC) includes the type of *S. tridynamum* var. *anoplocladum*. This agrees both with the plate which typifies *S. amazonium* and with the plant whose chromosomes were counted. If the very distinctive var. *anoplocladum* is in fact a variety of *S. tridynamum* Dun., as was judged by Dunal who described both *S. tridynamum* (Dun. *in* Lam., Encycl. Suppl. 3: 776, 1814) and *S. tridynamum* var. *anoplocladum*, then the earlier name *S. tridynamum* must take precedence over *S. amazonium*. The original description of *S. tridynamum* cites a Dunal plate and a Sessé and Mociño plate, neither of which was published, and neither of which could be examined at this time. *Solanum tridynamum* var. *anoplocladum* is a Mexican plant which has recently found its way into the Florida nursery trade. Dr. William Gillis reports that it is a weed in the plots at Fairchild Tropical Gardens, Miami.

Counts by THOMAS S. ELIAS, Missouri Botanical Garden.[2]

LEGUMINOSAE

Caesalpina crista L. 2n = 24. PANAMA. PANAMÁ: Playa del Palma, near San Carlos, *Lewis et al. 1503* (MO).

RUBIACEAE

Hamelia axillaris Sw. 2n = 24. PANAMA. CANAL ZONE: Madden Dam, Boy Scout Camp Road, *Dwyer & Elias 7491* (GH, MO, UC, US).

Hamelia patens Jacq. 2n = 24. PANAMA. SAN BLAS: Soskatupu, *Elias 1699* (MO), two plants.

Counts by WALTER H. LEWIS and ROYCE L. OLIVER, Missouri Botanical Garden.[3]

BIGNONIACEAE

Saldanhaea seemaniana O. Kuntze. 2n = 18. PANAMA. PANAMÁ: Between Río Pacora and Chepo, *Porter et al. 5150* (COL, MO, UC).

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[2] Present address: The Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

[3] Supported by National Science Foundation grant GB-5042.

COMMELINACEAE

Phaeosphaerion persicariaefolium (DC.) C. B. Clarke. 2n = 60.* PANAMA. CANAL ZONE: Vicinity of Madden Dam, *Lewis et al. 1813* (MO, UC).

Tripogandra floribunda (Hook. & Arn.) Woodson. 2n = 14.* PANAMA. CANAL ZONE: Farfan Beach, *Lewis et al. 49* (F, GH, K, MO, NY, UC, US).

CONVOLVULACEAE

Aniseia martinicensis (Jacq.) Choisy. 2n = 60.* PANAMA. HERRERA: Road from Chitre to Divisa, *Burch et al. 1360* (MO). Substitute for *Iseia luxurians* (Moric.) O'Donell, Chromosome numbers of phanerogams. 2, Ann. Missouri Bot. Gard. 54: 180, 1967.

Merremia macrocalyx (Ruiz & Pavon) O'Donell. 2n=28.* BRAZIL. Near Bahia-Minas Gerais border, between Pedra Azul and Vittoria da Conquista, seeds collected by Dr. Robert Dressler, voucher *Lewis 6798* (CAL, MO, NY, SMU).

EUPHORBIACEAE

Euphorbia ceratocarpa Ten. 2n = 26.* PORTUGAL. Cultivated at Missouri Botanical Garden (67-60-9), seeds from Jardim Botânico, Coimbra, voucher *Putman,* 1968 (MO).

Euphorbia graeca Boiss. & Sprunn. 2n = 32.* DENMARK. Cultivated at Missouri Botanical Garden (68-32-19), seeds from Hort. Bot. Hauniensis, Copenhagen, voucher *Putman,* 1968 (MO).

Euphorbia lagascae Spreng. 2n = 16.* DENMARK. Cultivated at Missouri Missouri Botanical Garden (68-32-22), seeds from Hort. Bot. Hauniensis, Copenhagen, voucher *Putman,* 1968 (MO).

Euphorbia platyphylla L. 2n = 28.* HUNGARY. Cultivated at Missouri Botanical Garden (68-23-4), seeds from Agrartudomanyi Egyetem Agrobot, Godolla, voucher *Putman,* 1968 (MO).

Euphorbia prunifolia Jacq. 2n = 16.* DENMARK. Cultivated at Missouri Botanical Garden (68-32-16), seeds from Hort. Bot. Hauniensis, Copenhagen, voucher *Putman,* 1968 (MO).

Euphorbia segetalis L. var. *portlandica* (L.) P. Cout. 2n = 18.* PORTUGAL. Cultivated at Missouri Botanical Garden (67-60-12), seeds from Jardim Botânico, Coimbra, voucher *Putman,* 1968 (MO).

IRIDACEAE

Sisyrinchium californicum (Ker) Dryand. 2n = 32.* CALIFORNIA. Seeds from University of California Botanical Garden, Berkeley; no voucher, but determination of immature plants verified.

LEGUMINOSAE

Erythrina atitlanensis Krukoff & Barneby. 2n = 42. GUATEMALA. SOLOLÁ: Between Santiago de Atitlán and San Pedro de Laguna, *Krukoff 1969-166* (NY) with count based on seedlings.

Erythrina × *bidwillii* Lindley. 2n = 42. CALIFORNIA. Cultivated at Missouri Botanical Garden from unrooted cuttings sent by Dr. Austin Griffiths, Jr.,

Department of Arboretum and Botanical Garden, County of Los Angeles, voucher *Lewis 7614* (GH, MO, NY).

Erythrina chiapasana Krukoff. 2n = 42. GUATEMALA. QUICHÉ: Near Cunen, *Krukoff 1969-211* (MO, NY) with count based on seedlings.

Erythrina cobanensis Krukoff & Barneby. 2n = 42. GUATEMALA. ALTA VERAPAZ: Near Tactic, *Krukoff 1969-195* (NY) with count based on seedlings.

Erythrina guatemalensis Krukoff. 2n = 42. GUATEMALA. ALTA VERAPAZ: Aldea Bangale (about 3 km from San Pedro Carcha), *Krukoff 1969-199* (NY) with count based on seedlings.

Erythrina sandwicensis Deg. 2n = 42. HAWAII. *Gillett s.n.* (location of voucher not known) with count based on seedlings (MBG 66-83-4); *Gillett 1983* (location of voucher not known) with count based on seedlings (MBG 66-83-5).

Erythrina subumbrans (Hassk.) Merrill. 2n = 42. ORIGIN UNCERTAIN. Cultivated, *Monsalud s.n.* (NY) with count based on seedlings (MBG 66-83-10).

Seeds of all species of *Erythrina* (except × *bidwillii*) were sent by B. A. Krukoff whose authoritative works on the genus are well known.

LILIACEAE

Nothoscordum bivalve (L). Britton. 2n = 18.* TEXAS. BOWIE COUNTY: Texarkana, *Suda 22* (MO). PANOLA COUNTY: Vicinity of Carthage, *Suda 18* (MO); Panola College campus, *Suda 20* (MO); Macedonia, *Suda 21* (MO).

LOGANIACEAE

Polypremum procumbens L. 2n = 20.* GUYANA. Vicinity of Georgetown, Atkinson Field Airport, *Robertson & Austin 269* (GH, MO, NY). Previous reports for this monotypic genus are all 2n = 22.

Strychnos panamensis Seem. 2n = 44.* GUATEMALA. SUCHITEPÉQUEZ: Chicacao, a few km from railroad station at Nahualate, alt. 500 feet, *Guillen 201* (NY). We thank B. A. Krukoff who sent seeds of this collection. Seeds were sown in our tropical greenhouses 25 November 1966 and germinated 27 April 1967.

PORTULACACEAE

Lewisia cotyledon (S. Watson) Robins. 2n = 28.* CALIFORNIA. SISKIYOU COUNTY: Klamath River cliffs, ca. 10 mi. N of Somes Bar, voucher *Lewis 6825* (MO). Seedlings were received from Dr. L. C. Hitchcock and grown at the Missouri Botanical Garden.

Montia parvifolia var. *flagellaris* (Bong.) C. L. Hitchc. 2n = 44.* OREGON: Coastal mountains, probably western slope near ocean, voucher *Lewis 6826* (MO). Seedlings were received from Dr. L. C. Hitchcock (who in turn received material from Carl English) and grown at the Missouri Botanical Garden. The typical variety is less robust and is diploid, 2n = 22 (Ann. Missouri Bot. Gard. 54: 181, 1967).

RUBIACEAE

Hedyotis biflora (L.) Lam. n = 18. SINGAPORE. Weed in Botanical Garden. Seeds were from S. R. J. White, progeny *Lewis 6693* (CAL, GH, MO).

Hedyotis caerulea (L.) Hook. n = 16. WEST VIRGINIA. TUCKER COUNTY: By river just above Black Water Falls, *Terrell 4131* (MO). This specimen is said to be an atypical form by its collector.

Hedyotis michauxii Fosberg. n = 16. NORTH CAROLINA. SWAIN COUNTY: Great Smoky Mountains National Park, road to Clingman's Dome, alt. 5500 feet, *Terrell 3961* (MO). WEST VIRGINIA. GREENBRIAR COUNTY: 1.5 mi. NW of Rupert, *Terrell 3989* (MO). TUCKER COUNTY: Black Water Falls, *Terrell 4162* (MO) (buds taken following cultivation at Silver Spring, Maryland).

UMBELLIFERAE

Oxypolis greenmanii Mathias & Constance. 2n = 28. Cultivated Missouri Botanical Garden (origin presumably Florida), voucher *Lewis 7613* (MO).

SOME NEW COMBINATIONS IN *PROTIUM* (BURSERACEAE)

In his monograph of *Protium* and several allied genera (Rec. Trav. Bot. Neerl. 39: 211–446. 1942), J. J. Swart used the name *P. neglectum* Swart to circumscribe several taxa of northern South America, Panama, and Costa Rica with sessile or rarely subsessile flowers. Cuatrecasas (Webbia 12: 375–441. 1957), however, has pointed out that *Protium neglectum* cannot be separated from the Peruvian and Bolivian *P. tenuifolium* (Engl.) Engl.

Protium tenuifolium ssp. *herbertii* (Cuatr.) D. M. Porter, *comb. nov.*

Basionym: *P. tenuifolium* var. *herbertii* Cuatr., Webbia 12: 407. 1957. [COLOMBIA: Santa Marta, *H. H. Smith 1741* (MO, isotype).]

P. neglectum var. *tenuifolium* Swart, Rec. Trav. Bot. Neerl. 39: 204. 1942.

Protium tenuifolium ssp. *mcleodii* (I. M. Johnst.) D. M. Porter, *comb. nov.*

Basionym: *P. mcleodii* I. M. Johnst., Sargentia 8: 164. 1949. [PANAMA: San José Island, *Johnston 557* (GH, holotype; MO, US, isotypes).]

Protium tenuifolium ssp. *sessiliflorum* (Rose) D. M. Porter, *comb. nov.*

Basionym: *Icica sessiliflora* Rose, N. Amer. Fl. 25: 259. 1911. [COSTA RICA: Santo Domingo de Golfo Dulce, *Tonduz 6989* (US, holotype; US, isotypes).]

P. sessiliflorum (Rose) Standley, Contr. U. S. Natl. Herb. 27: 224. 1928.

P. neglectum var. *panamense* Swart, Rec. Trav. Bot. Neerl. 39: 205. 1942. [PANAMA: Barro Colorado Island, *Bailey & Bailey 294* (F, holotype).]

P. neglectum var. *sessiliflorum* (Rose) Swart. *op. cit.* 39: 385. 1942.

The category subspecies, rather than variety, is used in the above combinations, as the taxa not only differ morphologically but also appear to be distinct geographically or ecologically. However, their morphological differences are not

sufficient to warrant specific recognition. The latter is not the case for the following taxon, included in the group by Swart. Here, the flowers differ from those in *Protium tenuifolium;* the petals are recurved rather than straight, and the stamens are exserted and spreading rather than included.

Protium robustum (Swart) D. M. Porter, *comb. nov.*
Basionym: *P. neglectum* var. *robustum* Swart, Rec. Trav. Bot. Neerl. 39: 204. 1942. [Surinam: Near Goddo, *Stahl 144* (U, holotype—not seen).]

These new combinations are based upon the examination of about 100 specimens of the taxa involved, including most types, at A, F, GH, MO, and US.—*Duncan M. Porter, Missouri Botanical Garden.*

Erratum: Ann. Missouri Bot. Gard. 56: 288, line 7. For "ad 10 cm longa" read "ad 4 cm longa."

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